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Habitat-based methods to estimate spawner capacity for chinook salmon in the Fraser River watershed

Méthodes axées sur l'habitat pour estimer la capacité d'accueil de saumons quinnats géniteurs dans le réseau fluvial du fleuve Fraser

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ABSTRACT

DFO requires escapement goals for chinook salmon populations to achieve objectives established by international agreements and domestic policy. In the Fraser River watershed, a stock-recruitment approach was used to generate an escapement goal for Harrison River chinook, however insufficient data exist for other Fraser chinook to use this method. In this report we focus on the development of habitat models to produce estimates of spawner capacity for chinook salmon returning to the Fraser River watershed. We plan to develop escapement goals from estimates of spawner capacity and management objectives.

To estimate spawner capacity, we used a stepwise process and initially stratified spawning systems by their biophysical characteristics. Within each stratum, we developed spawner density biostandards and spawner density-habitat relationships. Then, predictive relationships for numbers of spawners considering, and then alternatively ignoring, habitat quality estimated spawner capacity for spawning systems within each stratum. These stochastic models were applied within two of eight population strata as case studies to assist with evaluating the habitat-based approach.

Spawner habitat capacity models performed well overall, however additional information is required before these models will consistently generate realistic estimates of spawner capacity for chinook in high gradient and confined-channel spawning systems. Spawner-density gradient relationships were significant for several population strata but spawning capacity estimated from relationships with moderate coefficients of determination had high uncertainty. Estimates of spawner capacity were sensitive to scaling factors and high when scaling factors had positive bias. Additional work is required to improve the precision of the estimates of spawner capacity and to develop accurate scaling factors. Accordingly, the reported models and spawner capacity estimates are preliminary and based on a developing methodology.

RÉSUMÉ

Le MPO établit des objectifs d'échappée des populations de saumon quinnat afin d'atteindre les objectifs fixés par des accords internationaux et la politique nationale. Nous nous sommes servis d'une méthode stock-recrutement pour déterminer un objectif d'échappée pour le saumon quinnat de la rivière Harrison, mais les données disponibles sur les autres populations de saumon quinnat du réseau fluvial du Fraser sont insuffisantes pour appliquer cette méthode. Ce rapport porte sur la mise au point de modèles de l'habitat permettant d'estimer la capacité d'accueil de saumons quinnats géniteurs qui remontent dans le réseau fluvial du Fraser. Nous prévoyons déterminer des objectifs d'échappée à partir d'estimations de la capacité d'accueil de géniteurs et des objectifs de gestion.

Pour estimer la capacité d'accueil de géniteurs, nous nous sommes servis d'un processus séquentiel et avons d'abord stratifié les cours d'eau de fraie selon leurs caractéristiques biophysiques. Pour chaque strate, nous avons déterminé des normes biologiques de densité de géniteurs ainsi que des relations entre cette densité et l'habitat. Nous avons ensuite estimé la capacité d'accueil de géniteurs pour les cours d'eau de fraie de chaque strate en utilisant des relations prédictives qui, alternativement, tiennent compte ou non de la qualité de l'habitat. Nous avons appliqué ces modèles stochastiques à deux des huit strates de population en guise d'études de cas aidant à évaluer la méthode axée sur l'habitat.

En général, les modèles de la capacité de l'habitat à accueillir des géniteurs ont bien fonctionné, mais des données supplémentaires sont nécessaires pour que les modèles donnent systématiquement des estimations réalistes pour le saumon quinnat dans les cours d'eau de fraie à forte pente et au lit confiné. Les relations entre la densité de géniteurs et la pente étaient significatives pour plusieurs strates, mais les valeurs de capacité d'accueil de géniteurs estimées à partir de relations au coefficient de détermination modéré présentaient une incertitude élevée. Sensibles aux facteurs d'échelle, les estimations de la capacité d'accueil de géniteurs étaient élevées lorsque les facteurs d'échelle présentaient un biais positif. D'autres travaux sont nécessaires pour améliorer la précision des estimations de la capacité d'accueil de géniteurs et pour établir des facteurs d'échelle exacts. Les modèles et les estimations de la capacité d'accueil de géniteurs que nous présentons sont donc préliminaires puisqu'ils sont fondés sur une méthode en cours d'élaboration.

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1 Introduction

Preliminary spawner escapement goals were established for Fraser chinook in the 1980's. Stock assessments and stock-recruitment analyses by Healey (1982) and Starr (1982) indicated that stocks had declined substantially since the 1950's, but had only recently been overfished. Healey and Starr concluded that escapements during the early 1980's were likely only one-half of optimal levels. Goals were set for most populations as double the recent average escapements (1979-1982 period) primarily based on Starr's (1982) stock-recruitment analysis of one aggregate BC chinook stock. DFO proposed to assess the production response while spawning escapements increased and adaptively determine biologically based spawning escapement goals during a 15-year rebuilding program (CTC 1998).

A reference point is an estimated value derived from an agreed scientific procedure and/or an agreed model, which corresponds to a state of the resource, and/or of the fishery and can be used as a guide for fisheries management (FAO 1997). An escapement goal is a type of target reference point, which is selected to reflect the management objective for a group of fish and can be developed from an estimate of spawner capacity. The 1999 Pacific Salmon Treaty uses maximum sustained yield (MSY) or other biologically based escapement objectives as reference points for chinook. Domestically, the (draft) Wild Salmon Policy requires the establishment of reference points; these are also needed for Objective Based Fisheries Management and Integrated Fisheries Management Planning. In this report we focus on the development of habitat models to estimate spawner capacity for chinook salmon returning to the Fraser River watershed.

Throughout the rebuilding program, sufficient stock-recruitment data were collected from certain Key Streams to develop MSY escapement goals. However, the stock-recruitment approach requires stock-specific harvest rate data. Within the Fraser River watershed, since these data are available only for the Harrison River (Brown et al. 2001), alternate means of estimating target escapements were necessary. DFO began examining freshwater habitat-based methods to generate escapement goals for populations[1] for which a stock-recruitment approach was not possible.

When freshwater habitat capability models are used, the assumption is generally made that rearing or spawning habitat limits numbers. Freshwater rearing habitat probably does not limit most populations in the Fraser River watershed because of patterns of juvenile chinook behaviour and rearing habitat use. In the upper Fraser River, newly emerged chinook fry distribute themselves downstream of spawning areas throughout the natal stream, and within the Fraser River itself (Bradford and Taylor 1997). Some fry remain in their natal streams until they emigrate as smolts the following spring (Allan et al. 1995), whereas others appear to gradually migrate downstream through the watershed and rear in non-natal streams for short periods (Murray and Rosenau 1989; Scrivener et al. 1993). Juvenile chinook appear to disperse throughout all available rearing habitats, and it seems unlikely that freshwater rearing limits production for most populations since large amounts of productive, accessible rearing habitat exist throughout natal streams, non-natal tributaries to the Fraser River, the Fraser River mainstem, and its estuary (M. Bradford, DFO, pers. comm.).

We assume the bottleneck in freshwater production for many Fraser chinook salmon populations is spawning habitat availability, primarily because of our perception that juvenile rearing habitat does not appear to be limiting. In addition, we have observed that adult chinook appear to be displaced from high to lower quality spawning habitats during high escapements when high quality areas appear saturated.

[1] In this report, we refer to each major seasonal aggregation of chinook spawning in one major tributary as a population. However, since we have not examined degrees of isolation among these groups, they may or may not be equivalent to a population as defined in most genetic organizational schemes.

In theory, an optimal approach to assess freshwater chinook production would involve the collection of fry numbers from various watersheds over a wide range of escapements. However, cost and other considerations mean that this approach is not practical for Fraser chinook. We chose therefore to estimate spawning habitat capacity.

More commonly used habitat capability models, such as Physical HABitat SIMulation (PHABSIM), have had mixed results for chinook (Shirvell 1989; Williams 1996; Gallagher and Gard 1999). Some of these models had limited utility when applied to the rivers they were developed from and their utility for application to other rivers has rarely been assessed (Williams 2001). To ensure that predictions from these models are reliable, river- and site-specific data are normally required, and these would be cost prohibitive to collect for all Fraser River chinook populations. Thus, we set out to develop new models based on existing spawner density and habitat data that were less demanding on resources than methods such as PHABSIM. Our approach categorized rivers based on their biophysical similarity, then within each category the spawning habitat capability models were developed for application to the remaining rivers within the category.

The primary purpose of this report is to describe habitat-based methods to develop escapement goals for Fraser River chinook populations. Specifically, we aim to

1) describe a hierarchy to classify Fraser chinook spawning systems into biophysically similar groups;
2) describe several habitat-based models to predict spawning habitat capacity; and,
3) conduct two case studies as examples of applying these habitat-based approaches to assist with their evaluation.

2 Methods

2.1 Study Area

The Fraser River watershed, about 230,000 km^2 (Fraser et al. 1982), is the largest within British Columbia and occupies about 24% of the provincial landmass. The watershed contains 11 of the 14 provincial biogeoclimatic zones, which indicates the diverse range of soils, terrestrial vegetation, wildlife, and climate (Meidinger and Pojar 1991). The fish community is also diverse, with 52 species, and has a relatively complex zoogeographic history due to the formation of glacial lakes and altered drainage patterns during deglaciation (McPhail and Lindsey 1986; McPhail and Carveth 1994). Chinook spawn in about 70 main river basins and more than 100 named streams throughout the watershed (Figure 1).

2.2 Spawning System Stratification

The biophysical characteristics of chinook spawning systems vary considerably throughout the Fraser River watershed and it seemed unlikely that a single model would perform well for estimating spawning habitat capacity. Thus, we developed a qualitative classification hierarchy to stratify populations based on similar biophysical attributes. Then we investigated relationships between spawner density and habitat within strata and developed models to predict spawner capacity of streams within the respective strata (Figure 2). Model predictions were compared to maximum escapement estimates and provisional reference points were generated. A multivariate classification system was developed to investigate environmental relationships among spawning systems and to indicate where data pooling may be reasonable (Appendix 3).

2.2.1 Data Sources

Biophysical data were needed to characterize spawning systems and develop strata. Also, mean annual discharge (MAD) data were required for some models.

Physical attributes, such as the peak flow index, watershed area, and MAD were summarized by Rood and Hamilton (1995a-k) for the majority of chinook spawning systems throughout the Fraser watershed for standardized periods (1980-89 or 1981-90; Appendix 1). The peak flow index was the ratio of maximum daily flow for each year averaged over a standard period (peak flood) to MAD over a standard period, and provides an index of flow stability. Rood and Hamilton also described the procedures for estimating hydrologic characteristics of spawning systems without water gauging stations. However, some spawning systems were not considered by Rood and Hamilton, and when possible hydrologic data were obtained from the Water Survey of Canada HYDAT database. Hydrologic data were not available for systems in the Stuart Habitat Management Area.

Water temperature data were obtained from several DFO, Environment Canada, and private sources, however monitoring for most systems was discontinuous and few were monitored during similar time periods. We were unable to characterize the annual thermal regimes for most rivers, since most temperature monitoring focused on short periods chosen for other objectives. We calculated the average annual number of days with mean daily water temperatures exceeding 7°C (G7) as an indicator of the thermal regime and growth opportunity. We were unable to characterize the incubation thermal regime because very few systems were monitored during the winter. For some systems, we found considerable interannual variation in G7, thus we relied on G7 for qualitative descriptions.

Biological data were obtained from several sources. The peak spawning periods for 2000 and 2001 were obtained from aerial surveys conducted chiefly by us for most streams, however for those systems without aerial surveys the peak spawning periods were estimated from ground surveys or from people with local knowledge. The most frequent age of maturity was estimated from analyses of scale samples collected in the escapement and maintained in the SCALE database and scale archive library by the Scale Ageing Lab, Pacific Biological Station. Juvenile rearing habitat use descriptions were reported for most populations by DFO (e.g. DFO 1995, 1999), and was evident from scale ages. Migration timing through the lower Fraser River was obtained from Candy et al. (2002) and Fraser et al. (1982).

2.2.2 Tier 1: Lake Moderating Influence

The first tier separated populations into two groups based on biophysical characteristics (Figure 3). Systems with a large lake upstream generally had more stable flows than systems with small or no lakes upstream (Figure 4; Table 1; Appendix 1). Large lakes reduced the magnitude of flow changes (indicated by lower peak flow indexes, mean = 3.9 relative to systems with a small- or no-lake moderating influence, mean = 7.1).

Large lakes stabilize discharge by buffering flood effects, and reducing stream bank erosion and bedload movement compared to systems with highly variable discharge regimes (Montgomery et al. 1996). Thus, spawning habitat quality and egg-to-fry survival can be relatively higher in large-lake moderated systems than small- or no-lake moderated systems (Holtby and Healey 1986; Chapman 1988; Northcote and Larkin 1989; Montgomery et al. 1996;). Also, large lakes can trap fine sediments that adversely affect egg-to-fry survival (Chapman 1988). The stable discharge and reduced bedload movement in large lake moderated systems, such as Nechako and Chilko have contributed to the formation of extensive spawning 'dunes'. Spawning dunes are formed from generations of chinook spawning in the same area (Jeremovic and Rowland 1988). Often, they are the densest spawning areas and highest quality habitat because they contain little sand and fines, and presumably have high intragravel flow (Tutty 1986; Montgomery et al.

1996). In comparison, spawning dunes are rare among systems without large lakes upstream and limited to areas with stable discharge and little bedload movement.

Large lakes also stabilize thermal regimes and result in warmer fall and winter water temperatures than systems with a small- or no-lake moderating influence (Figure 5). The stable thermal regime of large-lake moderated systems contributes to less stressful incubation and rearing conditions than occur in small- or no-lake moderated systems, which experience rapid warming and cooling over short periods (Bjornn and Reiser 1991). In large-lake moderated systems, high winter water temperatures may reduce the extent of anchor and frazil ice formation and scour, thus contributing to higher quality incubation habitat and improved egg-to-fry survival (Bjornn and Reiser 1991).

The lake moderating influence appears to affect the life history of naturally spawning populations. Populations with a large-lake moderating influence return to the Fraser River and spawn later than populations with a small- or no-lake-moderating influence (Table 1). Systems with long, warm thermal regimes, measured by G7, were associated with a later peak of spawning activity ($r^2 = 0.55$; $P < 0.001$). Naturally spawning populations in systems with a small- or no-lake moderating influence were generally spring-run, with the peak of spawning activity during August or September (Candy et al. 2002). In comparison, systems with a large-lake moderating influence had summer- or fall-run populations with the peak of spawning activity during September, October, or November.

2.2.3 Tier 2: Juvenile Rearing Habitat

The second tier stratified populations based on the use of rearing habitats assuming that juvenile life history was indicative of freshwater habitat characteristics (Figure 3). Juvenile life history is associated with environmental conditions that influence the growth opportunity such that stream-type populations are associated with low growth opportunity and ocean-type populations with high growth opportunity (Healey 1983; Taylor 1990). The three major life history types for Fraser chinook (ocean type-immediate fry migrant, ocean type 60-150 d migrants, and stream type; Healey 1991) were represented in large lake moderated systems. Most Fraser watershed populations rear in rivers for one year before migrating to sea, and about six populations reared in lakes or rivers for 60 to 150 days before migrating to sea. The Harrison River fry emigrate from their natal area upon emergence and most rear in the Fraser River estuary. Juvenile life history was described for most populations in several technical reports (e.g. DFO 1995, 1999). However, for some populations we relied on scale age data from the SCALE database (DFO Vancouver) or scale library (Scale Ageing Lab, PBS, Nanaimo) to establish juvenile life history patterns. For populations with multiple juvenile life histories we used the most common pattern evident among fish sampled during the spawning period.

Systems with a small- or no-lake moderating influence were not partitioned further at the second tier since chinook in these rivers are almost all stream-type. Among systems with a large-lake moderating influence, the G7 was shorter for populations that reared in rivers for one year before migrating to the sea than populations that reared in rivers or lakes for 60-150 days (Table 1; Appendix 1). The population that reared in the estuary had the longest G7. Spawning systems with low growth opportunity were associated with stream-type life history and spawning systems with high growth opportunity were associated with ocean-type life history (Taylor 1990).

2.2.4 Tier 3: Physiography

The third tier further divided Fraser chinook into eight geographic groups based on their climatic and physiographic uniformity (Figure 3). Since these groups were developed to assist with modelling habitat capacity of rivers, they are not intended or proposed to be management groups. Meidinger and Pojar

(1991) described characteristics of provincial biogeoclimatic zones and the rest of this section includes descriptions based on their summaries. Peak-of-spawn timing and age-at-return are in Appendix 1.

Group 1 Lower Fraser includes the naturally spawning population in the Harrison River that primarily rears in the Fraser River estuary. The Harrison River lies with the Coastal Western Hemlock ecosystem, which is on average the rainiest biogeoclimatic zone in the province with cool summers and mild winters. The Harrison River had the most stable hydrologic regime (PFI = 2.8) and longest G7 (254 d) of all systems examined (Table 1). The Harrison River watershed is large and drains two large lakes, Harrison and Lillooet Lake. In the Harrison River, chinook return to the Fraser River mainly during September and the peak of spawning activity occurs in mid November. Harrison River chinook continue to be stocked into several tributaries of the Lower Fraser River, which were excluded from the spawning habitat capability modelling, since hatchery rearing space probably limits their production. The most common age at return is 0.3 (European age designation meaning zero winters spent in freshwater and 3 winters spent in the ocean).

Group 2 Middle Fraser includes the naturally spawning populations in areas with a large-lake moderating influence that rear in rivers for one year before migrating to sea. These populations spawn in four biogeoclimatic zones; Interior Douglas Fir, Interior Cedar-Hemlock, Sub-Boreal Pine-Spruce, and Sub-Boreal Spruce. Systems in the Interior Douglas Fir (Chilko, Portage and Seton) and Sub-Boreal Pine-Spruce (Taseko) ecosystems are in the rain-shadow of the Coast Mountains and experience a continental climate of warm, dry summers and cool winters. There is a strong glacial influence on the Taseko and Chilko rivers. Systems in the Interior Cedar-Hemlock ecosystem (Quesnel and Lower Cariboo) experience a continental climate of warm, dry summers and cool, wet winters. Systems in the Sub-Boreal Spruce ecosystem (Nechako and Stuart) experience seasonal extremes of temperature, with severe, snowy winters and warm, moist, and short summers. Group 2 Middle Fraser systems were generally large rivers in large watersheds with stable hydrologic regimes, and moderate G7 (167 d; Table 1). These populations return to the Fraser River during the summer and the peak of spawning activity occurs in September, except for Seton and Portage which appear to return in late summer and have a peak in spawning activity in late October. The most common age at return is 1.3.

Group 3 North Thompson includes the naturally spawning populations in areas with a large-lake moderating influence and large-river moderating influence that rear in rivers for one year before migrating to sea. The Clearwater and Mahood populations spawn in Interior Cedar-Hemlock ecosystems and the North Thompson River population spawns in the Interior Douglas Fir and Interior Cedar-Hemlock ecosystems. Group 3 North Thompson systems were generally large rivers in large watersheds with stable hydrologic regimes, but were without G7 data (Table 1). These populations return to the Fraser during the summer and the peak of spawning activity occurs in September. The most common age at return is 1.3.

Group 4 Lower-South Thompson includes the naturally spawning populations in areas with a large-lake moderating influence that rear in rivers or lakes for 60 to 150 days before migrating to sea. These populations spawn in Interior Cedar-Hemlock, Interior Douglas Fir, Ponderosa Pine and Bunchgrass ecosystems. The lower and South Thompson populations spawn in the deeply incised, arid valleys of the Interior Plateau that contain Bunchgrass and Ponderosa Pine ecosystems. Bunchgrass ecosystems experience hot, dry summers and moderately cold winters, whereas Ponderosa Pine ecosystems receive more precipitation during the winters than Bunchgrass ecosystems. These systems were large rivers in large watersheds with stable hydrologic regimes, and relatively long G7 (194 d; Table 1). These populations return to the Fraser during the late summer and the peak of spawning activity occurs in October. The most common age at return is 0.3.

Group 5 Lower Thompson includes the naturally spawning populations in areas with a small- or no-lake moderating influence that rear in rivers for one year before migrating to sea. These populations spawn in Interior Douglas Fir and Bunchgrass ecosystems, and water temperatures may exceed 25° C during summer months (Walthers and Nener 1997). These systems were small rivers in medium watersheds with variable hydrologic regimes, and moderately long G7 (177 d; Table 1). These populations return to the Fraser during the early spring and the peak of spawning activity occurs in August and September. The most common age at return is 1.2.

Group 6 Lower-Middle Fraser includes the naturally spawning populations in areas with a small- or no-lake moderating influence that rear in rivers for one year before migrating to sea. These populations spawn in six biogeoclimatic zones; Coastal Western Hemlock, Interior Douglas Fir, Interior Cedar-Hemlock, Sub-Boreal Pine-Spruce, Sub-Boreal Spruce, and Montane Spruce. The high elevation spawning areas of the Westroad system are in the Montane Spruce ecosystem and experience continental climate with cold winters and moderately short, warm summers. These systems were small rivers in moderate size watersheds with variable hydrologic regimes and moderate G7 (159 d; Table 1). These populations return to the Fraser during the spring and the peak of spawning activity occurs in August. The most common age at return is 1.3.

Group 7 Upper Fraser includes the naturally spawning populations in areas with a small- or no-lake moderating influence that rear in rivers for one year before migrating to sea. These populations spawn Interior Cedar-Hemlock, Sub-Boreal Spruce, and Engelmann Spruce-Subalpine Fir ecosystems. Spawning systems in the Engelmann Spruce-Subalpine Fir ecosystem experience cold, moist and snowy continental climate with long, cold winters. Group 7 systems were generally medium rivers in small watersheds with variable hydrologic regimes and the shortest G7 (110 d; Table 1). These populations return to the Fraser during the spring and the peak of spawning activity occurs in August. The most common age at return is 1.3.

Group 8 North-South Thompson includes the naturally spawning populations in areas with a small- or no-lake moderating influence that rear in rivers for one year before migrating to sea. These populations spawn in Interior Douglas Fir and Interior Cedar-Hemlock. These systems were generally medium rivers in small watersheds with variable hydrologic regimes and moderately short G7 (145 d; Table 1). These populations return to the Fraser during the spring and the peak of spawning activity occurs in August. The most common age at return is 1.3, however age 1.2 fish are common in Louis Creek and tributaries to Bessette Creek.

2.3 Habitat-Based Models

A consistent approach was used to develop spawning habitat models for each of the seven groups described in the classification hierarchy (Group 1 excluded; Figure 2). After stratification of the spawning systems, biostandards of maximum spawner densities on linear (per km) and area (per m^2) measurement scales were developed from recent escapement data, spawner distribution data, and spatial analysis of habitat availability (GIS). The biostandards and all model predictions excluded jacks (precocious males). Next, fish-habitat relationships were assessed, and models were developed to predict the spawner capability. These models relied on the amount of spawning habitat and spawner density biostandards to estimate the productive capability of each spawning system. We use the term spawner capability differently than spawner capacity and not synonymously. Spawner capability is the number of spawners a system would contain based on maximum observed densities. The spawner capability models were adjusted by a scaling factor that expanded the maximum observed spawner density biostandards to biostandards of spawning habitat capacity. In short, spawner capacity models predicted the spawner carrying capacity for each system. In most cases, the capacity would be expected to exceed the capability

unless the system was at carrying capacity during the period of record. Finally, reference points would be developed based on management objectives and predicted spawner capacity.

Nine rivers were selected to investigate relationships between spawner density and habitat. We chose Bowron, Willow, Nechako, Chilko, Clearwater, Raft, Lower Shuswap, and Nicola rivers, and Elkin Creek because they represented the range of biophysical conditions throughout the watershed, were regarded as having the highest quality escapement estimates within their groups, and some had existing field programs. For each of these systems recent escapements were estimated with consistent methods and most had good viewing conditions for aerial or foot surveys. For instance, intensive mark-recapture programs have been conducted on the Nicola River since 1995 (Bailey et al. 2000), Lower Shuswap River since 2000, and area-under-the-curve (AUC) programs on the Nechako River since 1987 (Hill and Irvine 2001).

2.3.1 Biostandards

Spawner density biostandards were estimated for spawner index strata for each of the nine streams. Each year, spawning systems were surveyed on three or more days during the peak of the spawning period, and spawner numbers were recorded by spawner index strata. The spawner index strata were bounded by distinct landmarks intended to clearly identify the stratum start- and end-points. They were not intended to index areas of similar habitat quality, and often, they contained variable quality spawning habitat.

The spatial distribution of spawners was estimated from

$$\hat{N}_{i,j,k} = \frac{P_{i,j,k}}{\sum_{j} P_{i,j,k}} \hat{N}_{i,k}, \qquad (1)$$

where $\hat{N}_{i,j,k}$ was number of spawners in year *i* in spawner index stratum *j*, in river *k*, $\hat{N}_{i,k}$ was the annual escapement estimate, and P was the count of spawners on the survey date with the highest spawner count (Table 2). Spawner counts were omitted when they included several strata. Data for the Bowron, Willow, Chilko, Clearwater, Lower Shuswap, and Nicola Rivers and Elkin Creek were from the chinook escapement database maintained by BC Interior Area, DFO, Kamloops. Data for the Raft River were summarized by Galesloot (1996, 1997, 1998, 1999, 2000a, 2000b, 2002) and for Nechako River by (Hill and Irvine 2001) and unpublished data maintained by the Nechako Fisheries Conservation Program, DFO, Prince George.

For each stratum, annual spawner estimates were compared among years and the maximum estimate was the maximum observed spawner density. For the linear biostandards, spawner density ($\hat{D}_{j,k,l}$) corresponding to measurement scale *l* was estimated with

$$\hat{D}_{j,k,l} = \frac{\max \hat{N}_{j,k}}{L_{j,k}}, \qquad (2)$$

where $\max \hat{N}_{j,k}$ was the maximum number of spawners in the index stratum over the available time series of spawner surveys, $L_{j,k}$ was the length of a centerline for the spawner index stratum generated from 1:20,000 Terrain Resource Information Map (TRIM) 3-D spatial data following the method described by Williams et al. (1999). For the area measurement scale, spawner density was estimated from

$$\hat{D}_{j,k,l} = \frac{\max \hat{N}_{j,k}}{L_{j,k} \bullet \hat{W}_{j,k}}, \qquad (3)$$

where $\hat{W}$ was the wetted width during the late summer low flow period calculated from

$$\hat{W}_{j,k} = 5.42 \bullet MAD_{j,k}^{0.523}, \quad (4)$$

and *MAD* was the naturalized MAD (r^2=0.93; CV=0.12; Tautz et al. 1992). This relationship was developed from 119 reaches from 47 different streams in British Columbia. Naturalized MAD was the observed MAD adjusted for water removals and data were obtained from Rood and Hamilton (1995a-k) or the HYDAT database for Water Survey of Canada stations. Rood and Hamilton estimated MAD at stream mouths and we adjusted the stream mouth MAD to account for inflows from tributaries with *MAD* reported by Rood and Hamilton to estimate MAD_j.

2.3.2 Habitat Data Sources

We found few spatially referenced databases containing appropriate macrohabitat parameters and developed with consistent methods and scale throughout the Fraser River watershed. The best databases were the 1:50,000 scale Watershed Atlas and 1:20,000 scale TRIM (Geographic Data BC, BC Ministry of Environment, Lands, and Parks) and both had limitations, advantages, and disadvantages. The TRIM database was chosen because it contained several geomorphological and land use features including the location and elevation of the stream bank, which was used to calculate stream gradient, as well as other spatial features (MELP 1992). Initially, we focused on stream gradient as a potential descriptor of habitat use because it was significantly correlated with salmon and trout abundance (Kozel et al. 1989; Sharma and Hilborn 2001; Press et al. 2002) and was a useful predictor of trout presence and absence (Kruse et al. 1997). Gradient influences stream energy, which then interacts with geomorphology and terrestrial features to form fish habitats (Montgomery et al. 1999; Isaak et al. 1999). At a course scale, fish habitats can be categorized by channel morphology or pool frequency (Montgomery et al. 1995), which were related to chinook and coho redd density in the Skagit River (Montgomery et al. 1999).

The TRIM database contains other physical habitat and land use characteristics that may be related to spawning habitat quality (Sharma and Hilborn 2001; Press et al. 2002), however this information was not available for this report yet could be considered in future analyses. Also, other databases containing hydrologic or geologic information could be considered in future analyses. Furthermore, microhabitat variables such depth, velocity, and flow are often used to describe spawning habitat suitability (Williams 2001), however these data do not exist for all streams and would be cost prohibitive to attain.

For TRIM, elevation data exist for each point along the stream bank, but not the water surface. Stream gradient for each spawner index stratum was estimated from a generated centerline using stream bank 3-D spatial data from TRIM (Williams et al. 1999). The Watershed Atlas contained gradient data for macroreaches, but they were unlikely to correspond to spawner index strata, the latter bounded by landmarks (e.g. bridges, buildings, and confluences), because macroreaches were determined from stream gradient, discharge, substrate type, channel type, position in the landscape, and valley flat width (MELP 2000). Also, elevation data were not available for points along the land-water boundary in the Watershed Atlas.

There may be inconsistencies in the land-water boundary definition in TRIM throughout the Fraser River watershed. Inconsistencies can result from air photos taken at different times of the year, in different years, or if different interpreters were used. The time of year and year can influence the interpretation of the stream bank when rivers are at different stage heights. In general, the variability will be larger among watersheds than within because air photographs were usually taken around the same time and interpreted by the same person for areas close in proximity.

The length and gradient measurements of the spawner index strata were influenced by the positional accuracy of TRIM points (nodes) and errors associated with assigning stratum boundaries. Each point has

a horizontal accuracy of ±10 m and vertical accuracy of ± 5 m (MELP 2000). We reduced errors associated with assigning stratum boundaries by relying on a combination of stratum boundaries labeled on 1:50,000 scale NTS maps by field staff and GPS recordings at stratum boundaries.

2.3.2.1 Stream Network Models

Spatial models were built to provide the length and gradient data for each stream using TRIM data and methods are described in detail by Williams et. al. (1999). Right bank, left bank, and single line rivers and lakes were used to build the network, and roads and bridges were for spatial reference. Three dimensional (3-D) stream networks were constructed with data from multiple map sheets. A 3-D centerline was generated between the right and left banks and through the lakes. The networks were sectioned according to boundaries determined from field data as well as into ~1 km strata within the boundaries of chinook distribution. Length was calculated for the centerline of each stratum. Gradient was calculated from the 3-D centerline in an upstream direction as rise/length. This was calculated using the z value for the upstream and downstream data points for each stratum to calculate rise, and all data points to calculate length.

2.3.3 Spawner Capability

Spawner capability models predict the number of spawners a system would contain based on maximum observed densities. Predictions from spawner capability models would be less than spawner capacity when observed densities exclude spawner densities that saturated the spawning habitat within the spawner survey strata. Observed spawner densities may exclude the densities that occur at spawning habitat capacity because the period of record was short for most streams.

2.3.3.1 Habitat Suitability Models

To assess spawning habitat suitability we assumed that spawner density indicated spawning habitat quality within a river where high and lower quality habitat corresponded to high and lower spawner densities, respectively. For each river, we examined scatterplots of spawner density (per km and per m^2) and gradient for spawner index strata. In the literature, habitat suitability curves have often been fit by interpolation, non-quantitative methods, or polynomial regression (e.g. Raleigh et al. 1986; Amiro 1993). However, we focussed on developing predictive relationships and considered several continuous, statistical distributions such as the normal, lognormal, gamma, logistic, and weibull. Polynomial regression was not appropriate because it can develop relationships that predict negative spawner densities, or relationships with multiple maxima or minima, which were conceptually unreasonable. We chose the normal distribution because it was suitable for continuous gradient data, would not predict negative spawner density, has only one maximum point, had described habitat suitability relationships in some studies, and was the model with the lowest log-likelihood for the Nicola River data, which was the data set we had most confidence in.

The relationship among the maximum observed spawner density and gradient was estimated by fitting a normal curve using the maximum likelihood method with normally distributed error (Hilborn and Mangel 1997),

$$\hat{D}_{j,k,l} = \hat{A}_{k,l} \bullet \left(\frac{1}{\sqrt{2 \bullet \pi \bullet \hat{S}_{k,l}^2}}\right) \bullet \left(e^{\left(-\frac{(G_{j,k}-M_{k,l})^2}{2 \bullet \hat{S}_{k,l}^2}\right)}\right), \qquad (5)$$

where $\hat{D}_{j,k,l}$ was the spawner density in measurement scale *l* in spawner index stratum *j* of spawner index river *k*, G was the gradient, $\hat{A}$ was the area under the curve, and $\hat{M}$ and $\hat{S}$ were the estimated mean and standard deviation of the curve, respectively. The coefficient of determination and ANOVA were used to assess the significance of the spawner density-gradient relationship. Negative estimates of gradient existed for some strata. They resulted when the stream bank increased in elevation between strata boundaries along the course of a river. Stream bank gradient data were used as a proxy for stream gradient, and since streams cannot flow uphill, the negative values were considered errors and pooled with zero gradient values. Standard errors of $\hat{A}_{k,l}$, $\hat{M}_{k,l}$ and $\hat{S}_{k,l}$ were estimated with non-linear regression with the maximum likelihood estimates used as the initial parameters. Habitat suitability curves were examined for area and linear spawner densities.

Spawning habitat capability was estimated with linear and area models (Figures 6 and 7, respectively). Stream networks were generated for each river and these were partitioned into ~1 km sequential prediction strata throughout the chinook distribution described in the Fisheries Inventory Summary System (FISS; DFO 2001), excluding identified ephemeral rearing habitat. For each prediction stratum, gradient was estimated from a generated 3-D centerline from TRIM spatial data (Williams et al. 1999). For the linear model, spawner density was predicted from the linear habitat suitability curve. The spawner capability ($\hat{C}_{l,m,n}$) for prediction stratum *m* of prediction river *n* was estimated from

$$\hat{C}_{l,m,n} = \hat{D}_{l,m,n} \bullet L_{m,n}, \tag{6}$$

where $\hat{D}$ was spawner density from Equation 5, and L was the prediction stratum length. Spawner habitat capability estimates were summed over all prediction strata to estimate the total ($\hat{C}_{l,n}$),

$$\hat{C}_{l,n} = \sum_{m} \hat{C}_{l,m,n}. \tag{7}$$

The area model was similar in structure to the length model, but relied on the area-based habitat suitability curve, Equation 5, to predict spawner density ($\hat{D}_{l,m,n}$),

$$\hat{C}_{l,m,n} = \hat{D}_{l,m,n} \bullet L_{m,n} \bullet \hat{W}_{m,n}. \tag{8}$$

Wetted width ($\hat{W}$) was estimated with Equation 4 and *MAD* and the spawning habitat capability estimates were summed over all prediction strata to estimate the total with Equation 7.

We developed 95% confidence limits of the spawning habitat capability for each stream with a parametric bootstrap procedure (Figure 8). For habitat suitability curves, the $\hat{A}_{k,l}$, $\hat{M}_{k,l}$ and $\hat{S}_{k,l}$ parameters were assumed to follow a normal distribution with the mean and standard error of the parameters estimated from the non-linear regression analysis. For each bootstrap sample, a habitat suitability curve was developed by randomly drawing, with replacement, one $\hat{A}_{k,l}$, $\hat{M}_{k,l}$ and $\hat{S}_{k,l}$ from their respective distributions and substituted into Equation 5. Then $\hat{D}^{*}_{l,m,n}$ and $\hat{C}^{*}_{l,m,n}$ were estimated with Equations 5 and 6 and repeated for each prediction strata, and $\hat{C}^{*}_{l,n}$ was estimated with Equation 7. For the stream spawner capability estimates, and following bootstrap analyses, the procedure was repeated 10,000 times creating the distribution $\hat{F}(\hat{C}^{*}_{l,n})$ and 95% confidence limits were estimated from the 2.5th and 97.5th percentiles (Efron and Tibshirani 1993). A similar parametric bootstrap procedure was used to estimate confidence limits for $\hat{C}^{*}_{l,n}$, with $\hat{A}_{k,l}$, $\hat{M}_{k,l}$ and $\hat{S}_{k,l}$ parameters, from the area habitat suitability curve

used to estimate $\hat{D}^{*}_{l,m,n}$ (Figure 9). Also, a wetted width measurement ($\hat{W}^{*}_{m,n}$) was drawn randomly, with replacement from a lognormal distribution, with an arithmetic mean equal to the width from Equation 4 and a coefficient of variation (CV) of 0.12, since regression data were not available to calculate logarithmic parameters. $\hat{C}^{*}_{l,,m,n}$ was calculated with Equation 8 and substituted for $\hat{C}_{l,m,n}$ in Equation 7 to calculate $\hat{C}^{*}_{l,n}$. The bootstrap analyses created the empirical distribution $\hat{F}(\hat{C}^{*}_{l,n})$.

2.3.3.2 Spawner Density Models

Spawner density models were developed to predict spawner capability from the amount of available spawning habitat. Unlike the spawning habitat suitability models, the spawner density models did not estimate spawner density from spawning habitat quality relationships and assumed uniform spawning habitat quality. Instead, spawner density biostandards for the linear model ($\hat{D}_{k,l}$) were estimated with

$$\hat{D}_{k,l} = \frac{\sum_{j} \max \hat{N}_{j,k}}{\sum_{j} L_{j,k}}, \tag{11}$$

and the area model ($\hat{D}_{k,l}$) with

$$\hat{D}_{k,l} = \frac{\sum_{j} \max \hat{N}_{j,k}}{\sum_{j} L_{j,k} \bullet \hat{W}_{j,k}}. \tag{12}$$

When the maximum escapement estimate exceeded the sum of the maximum strata escapements, the maximum escapement estimate was substituted for the sum of the strata escapement estimates to develop spawner density biostandards.

Spawning habitat capability was estimated with area and linear models. Each prediction river *n* was partitioned into ~1 km prediction strata *m* following methods for the habitat suitability models. Spawning habitat capability was estimated with the linear model,

$$\hat{C}_{l,n} = \hat{D}_{l,k} \bullet \sum_{m} L_{m,n}, \tag{13}$$

and area model,

$$\hat{C}_{l,n} = \hat{D}_{l,k} \bullet \sum_{m} (L_{m,n} \bullet \hat{W}_{m,n}). \tag{14}$$

Confidence intervals (95%) were developed for the area spawner capability estimates following a bootstrap analysis, but not for the linear spawner capability estimates. For the area model, we estimated 95% confidence intervals for spawner capability by randomly drawing, with replacement a wetted width measurement ($\hat{W}^{*}_{m,n}$) from a lognormal distribution, with an arithmetic mean equal to the width from Equation 4 and CV of 0.12. The bootstrap analyses created the empirical distribution $\hat{F}(\hat{C}^{*}_{l,n})$.

2.3.3.3 Model Comparisons

To assess the overall fit of the habitat suitability and spawner density models, the likelihood of each model calculated for all nine streams (pooled) was compared using the Akaike Information Criterion

(AIC), since the models were not nested (Hilborn and Mangel 1997). For these comparisons, the spawner density models were based on the mean density of the spawner survey strata for the nine streams. These comparisons assume spawner densities are independent among locations (survey strata and rivers).

2.3.4 Spawner Capacity

Spawner capacity models predict the spawner carrying capacity for each system. Spawner capacity is the number of spawners required to fully saturate the available spawning habitat within the system. In most cases, the capacity would be expected to exceed the capability unless the system was at carrying capacity during the period of record.

Patches of high quality spawning habitat exist within the study streams at measurement scales smaller than the spawner index strata. For example, at the channel unit scale (Hawkins et al. 1993) the best quality habitat often occurs within riffles and the transition zone between pools and riffles, and lower quality habitat occurs within pools, runs, and rapids. We assume spawning habitat selection is density dependent, and that spawners would optimally occupy the high quality habitat at most escapement levels except for low levels when the recruit-to-spawner ratio (R:S) is highest and compensatory density dependent effects are minimal. As spawner abundance increases, high quality habitat will become saturated. Spawners will be displaced to lower quality areas where R:S will average less than in higher quality areas. The disparity in R:S among high and lower quality areas is evident from the competition for and territoriality at the spawning areas, and we presume spawners benefit, in terms of fitness, by successfully competing for high quality spawning areas. As the total spawner abundance levels for the population increase the average R:S for the population will decrease and become 1 when the high and low quality habitats are fully saturated. Spawner abundance above this level would have an average R:S less than 1 for the population. Thus, the highest spawner densities in the high quality habitat should represent the spawning density where the high quality habitat is saturated. These hypotheses are unsubstantiated, and supporting analyses would be beneficial.

For the Nicola and Lower Shuswap rivers, spawner densities were measured in the high spawning activity areas. On the Nicola River, redd density was measured in seven sections, about two weeks after the peak of spawning activity in 2000, that were considerably shorter (~36 m) than the spawner index strata (~16 km). Field staff working on the mark-recapture program (Bailey et al. 2000) identified the sections, measured the wetted area and counted redds. Spawner density was estimated assuming 2 spawners/redd. On the Lower Shuswap River, spawner density was measured in three sections, about three days before the peak of spawning activity in 2001, that were shorter (~1 km) than the spawner index strata (~3 km). Field staff working on spawner-residence-time and mark-recapture programs identified sections, marked off section boundaries, and counted spawners in each section during aerial surveys. The percentage of spawners within each section was estimated from aerial spawner surveys by dividing the section count by the total, which was multiplied by the escapement to estimate the number of spawners in each section. The length of the sections was measured by GPS and wetted width was calculated with Equation 4.

Spawner capacity models were developed by adjusting the spawner capability models by a scaling factor that expanded the observed spawner density biostandards to biostandards of spawning habitat capacity. The scaling factors were calculated from the ratio of the highest spawner densities measured in the high spawning activity areas to the maximum spawner densities predicted from the habitat suitability model. Thus, these scaling factors were based on the assumption that habitat within the spawner survey strata was the type of habitat surveyed in the high spawning activity areas. More representative scaling factors could be developed by repeating the process for channel geomorphic units (Hawkins et al. 1993), and calculating a scaling factor weighted by the amount of each channel geomorphic unit in the stream.

2.3.4.1 Scaled Habitat Suitability Models

The habitat suitability models described the relationships among gradient and the maximum observed spawner density, and predictions from this relationship were presumably less than the spawning habitat capacities. To estimate the relationships for spawning habitat capacity, the habitat suitability curves were increased by a scaling factor, which adjusted the maximum spawner density on the habitat suitability curve to the maximum density observed in the small river sections. The scaling factor ($\hat{R}$) increased the area under the habitat suitability curve and expanded the curve to estimate spawning habitat capacity,

$$\hat{A}_{k,l,s} = \hat{R}_{k,l} \bullet \hat{A}_{k,l}. \quad (9)$$

The mean and standard deviation of the curve remained unchanged and retained the original shape and location.

Scaling factors were the ratio of the maximum spawner density measured from small river sections to the maximum spawner density on the habitat suitability curve,

$$\hat{R}_{k,l} = \frac{\max \hat{D}_{empiricaldata,k,l}}{\max \hat{D}_{habitatsuitabilitycurve,k,l}}. \quad (10)$$

Spawning habitat capacity was estimated with area and linear models and confidence intervals were calculated with the methods described for the habitat suitability curves, although spawner density was estimated from the scaled habitat suitability curves.

2.3.4.2 Scaled Spawner Density Models

The scaled spawner density models had similar structure to the spawner density models, but relied on scaled spawner density biostandards. The scaling factors developed for the scaled habitat suitability curves were used to increase the biostandards from the spawner density models, and ideally this model would rely on scaling factors that better represent the composition of channel units. Then, the scaled spawner density biostandards were substituted into Equations 13 and 14 for the linear and area models, respectively, to calculate spawner capacity. For the area model, the scaled area spawner density was substituted into the bootstrap analysis to develop 95% confidence intervals for spawner capacity.

2.5 Case Study Examples

Two case studies were used to demonstrate the application of habitat-based methods for estimating spawner capacity for Fraser River chinook salmon. The first case study included spawning systems in the Lower Thompson basin (Group 5) with a small- or no-lake moderating influence on hydrology and juveniles that rear in rivers for one full year before smoltification. The second case study included systems in the Lower and South Thompson basins (Group 4) with a large-lake moderating influence on hydrology and juveniles that rear in rivers or lakes for 60-150 days before smoltification.

For each system, we estimated the amount of spawning habitat available and the gradient for each ~1 km prediction strata using TRIM for the distribution of chinook salmon described by FISS (DFO 2001). Spawning habitat capability was determined from the habitat suitability and spawner density models, and spawning habitat capacity was estimated from the scaled habitat suitability and spawner density models. Spawning habitat capability and capacity were compared to maximum escapement estimates by calculating the relative deviation expressed as a percentage of the maximum escapement estimates. Confidence limits (95%) were developed for habitat capability and capacity of each system using the bootstrap analyses described for the respective models.

3 Results

3.1 Habitat-Based Models

3.1.1 Spawner Capability

3.1.1.1 Habitat Suitability Models

For Group 2 Middle Fraser systems, there was a good relationship between the maximum observed spawner density and gradient for Chilko River (Figure 10c), but no apparent pattern for Nechako River (Figure 11d; Table 3). Chilko River had six strata with spawner density and gradient data, and eight years with spawner counts by strata. Escapements were estimated with the peak count (1992-1999) and AUC methods (2000-2001). The sum of the maximum strata escapements exceeded the highest escapement estimate by 30%, which indicated the habitat suitability curve included years of relatively high spawner densities over the time series (Table 4).

Considerably more spawner count data existed for Nechako River than Chilko River, but the Nechako River had lower contrast on the gradient axis than Chilko River. Nechako River had 16 strata with spawner density and gradient data, and 17 years with spawner counts. Escapements were estimated with the peak count (1984-1986, 2001) and AUC methods (1988-2000). Stratum spawner counts were not available for 1987. For 2001, the peak count method was used because survey intervals were too sparse for accurate AUC escapement estimates, due to the grounding of all flights following September 11. The sum of the maximum strata escapements exceeded the highest escapement estimate by 3% (Table 4). On average, the strata were longer in Nechako River (8.4 km) than Chilko River (6.8 km), and the Nechako was very low gradient (0.0005) compared to Chilko (0.0104).

For Group 3 North Thompson systems, there were too few data to adequately assess the relationship between the maximum observed spawner density and gradient (Figure 11a). The Clearwater and Mahood had four strata (Clearwater 3 and Mahood 1) with spawner density and gradient data, and seven years with spawner counts. Escapements were estimated with the peak count (1995-1999) and AUC methods (2000-2001). The sum of the maximum strata escapements exceeded the highest escapement estimate by 49% (Table 4). However, the maximum spawner estimate for the Mahood River was less than the highest escapement estimate. On average, the strata were very long in the Clearwater River (23.2 km) and the river had moderate gradient compared to Chilko and Nechako rivers.

For Group 4 Lower-South Thompson systems, there was a good relationship between the maximum observed spawner density and gradient for the Lower Shuswap River (Figure 10b; Table 3). There were 11 strata with spawner density and gradient data, and seven years with spawner counts. Escapements were estimated with the peak count (1995-1999) and mark-recapture methods (2000-2001). The sum of the maximum strata escapements was about equal to the highest escapement estimate (Table 4). Furthermore, most strata were relatively short, about 3.4 km, compared to those for the Chilko, Nechako and Clearwater rivers. Lower Shuswap River had a low gradient, similar to the Nechako River.

For Group 5 Lower Thompson systems, there was a good relationship between the maximum observed spawner density and gradient for the Nicola River (Figure 10a; Table 3). There were six strata for the Nicola River, one for the lower Coldwater and one for lower Spius Creek with spawner density and gradient data, and seven years with spawner counts. The datum for Coldwater River occurred within the spawner density-gradient data from Nicola River and was retained for analyses, whereas the datum for Spius Creek had high gradient and did not appear to follow the relationship for the Nicola River, and was excluded. Escapements were estimated with mark-recapture from 1996 to 2001. The sum of the

maximum strata escapements exceeded the highest escapement estimate by 7% (Table 4). On average, the Nicola River strata were long (17.0 km) and the river had moderate gradient.

For Group 6 Lower-Middle Fraser systems, there was a moderate relationship between the maximum observed spawner density and gradient for Elkin Creek (Figure 10d; Table 3). There were six strata with spawner density and gradient data, and four years with spawner counts. Escapements were estimated with the peak count method from 1995 to 2001. The sum of the maximum strata escapements was about half the highest escapement estimate (Table 4). On average the strata were short (3.2 km) and the creek had moderate gradient.

For Group 7 Upper Fraser systems, there were too few data to adequately assess the relationship between the maximum observed spawner density and gradient (Figures 11b and c). Willow River had four strata with spawner density and gradient data, and four years with spawner counts. Escapements were estimated with the peak count (1998, 1999 and 2001) and AUC methods (2000). The sum of the maximum strata escapements was about equal to the highest escapement estimate (Table 4). On average, the strata were moderately long (13.2 km) and the river had moderate gradient.

For Bowron River, there were too few strata (4) to adequately assess the relationship between the maximum observed spawner density and gradient (Figure 11b). There were nine years with spawner counts and escapements were estimated with the peak count (1991-2000) and AUC methods (2001). The sum of the maximum strata escapements was less than the highest escapement estimate (Table 4). On average, the strata were long (37.9 km) and the river had moderate gradient.

For Group 8 North-South Thompson systems, there was a fair relationship between the maximum observed spawner density and gradient for Raft River, but one datum was highly influential (Figure 10e; Table 3). There were eight strata with spawner density and gradient data, and seven years with spawner counts. Escapements were estimated with the AUC method from (1995-2001). The sum of the maximum strata escapements exceeded the highest escapement estimate by 40% (Table 4). On average, the strata were very short (~0.5 km) and the river had moderate gradient.

The spawning habitat suitability curves had consistent characteristics among the systems examined. The Kolmogorov-Smirnov one-sample tests indicate that residuals were normally distributed for all the curves (Table 3) and were fairly evenly distributed around zero when plotted with gradient, yet positive residuals were common at high gradients. The explanation for this is that these reaches frequently contained a variety of habitat including areas with gradient suitable for spawning. The gradient was high on average because physical features such as falls or canyons were stratum boundaries. Spawner densities were also variable at low gradients and spawner density was influenced by factors other than gradient. For example, on the Lower Shuswap River the higher spawner densities among low gradient strata were associated with spawning habitat created by tributary streams that delivered spawning gravel to the mainstem, which constricted the channel and increased water velocity.

The habitat suitability curve parameters were influenced by the range of spawner escapements and number of years with escapement estimates. The range of spawner escapements was probably more influential on the width of the curve than its location (mean gradient). It appears that density dependent pressures resulted in the use of less suitable spawning areas at high escapements. When escapements varied by an order of magnitude in Nechako and Nicola rivers, the relative spawner distribution varied significantly and relatively more fish appeared to use lower quality spawning habitat (Figure 12; Nechako River, chi-square = 530, $P<0.001$; Nicola River, chi-square = 303, $P<0.001$). If chinook spawning habitat use was independent of density, then the relative distribution of spawners would be similar for high and low escapements unless density independent factors had a significant influence on spawning distribution. Bradford (1994) reported that spawner distribution was correlated with discharge

in the Nechako River, but the significance of the relationship depended on three data points from low flow years (1978-1980). If density independent factors do not significantly influence spawning habitat use, the habitat suitability curves developed from data obtained during years of low escapements would identify the high quality habitat, but under-estimate the potential utility of lower quality habitat and result in a narrow curve. Furthermore, high escapements may not have been observed in systems with short time series.

In addition, the number and size of spawner index strata influence the data available for estimating habitat suitability curves. For systems with few survey strata we were unable to describe the spawner density-gradient relationship, whereas for other systems the contrast in the gradient range for spawner index strata may be insufficient to describe the ascending or descending limbs of the curve. Longer strata probably include wider ranges of spawning habitat quality than shorter strata and may inadequately represent the spawner density-gradient relationship. Shorter survey strata may be more influenced by variability in elevation data than longer survey strata. For example, the short survey strata in Raft River contributed to large differences in calculated gradient among strata when the rise was 0.5 m.

3.1.1.2 Spawner Density Models

The spawner density biostandards were less than the maximum spawner densities measured in the spawner index strata because the biostandards were based on all the available spawning habitat and some rivers included large areas of very low spawner density. Linear spawner density biostandards were highest in Chilko River and lowest in Willow River, whereas area spawner density biostandards were highest in Raft River and lowest in Nechako River (Table 4).

3.1.1.3 Model Comparisons

The habitat suitability and spawner density models differed in overall fit to the linear and area biostandards and no model consistently performed better than the other did. The spawner density model (AIC = 493) performed better than the habitat suitability model (AIC = 497) for linear biostandards, but the habitat suitability model (AIC = 257) performed better than the spawner density model (AIC = 266) for area biostandards.

3.1.2 Spawner Capacity

3.1.2.1 Scaled Habitat Suitability Models

Scaled habitat suitability curves were developed for the Nicola and Lower Shuswap rivers, but have not been developed for the remaining systems.

For the Nicola River, the scaled habitat suitability curves were considerably higher than the original curves (Figure 13). The maximum spawner densities were about 3.5 times higher than the maximum densities on the habitat suitability curves, and scaling factors ranged from 0.9 to 3.9 (Table 5). The large scaling factors may have resulted from different measurement scales. Redd densities were measured in very short strata (12-44 m) and areas of high redd density, whereas the habitat suitability curve strata were much longer (8.6-28.6 km) and included areas of high and low redd density.

The scaling factors were smaller for the Lower Shuswap River than the Nicola River. The highest spawner densities estimated for the Lower Shuswap River were 1.6 times higher than the maximum densities on the habitat suitability curves, and the measurement scales were more similar than those for the Nicola River. Spawner densities were estimated in strata ranging from 0.15 to 1.4 km, whereas the

habitat suitability curve strata ranged from 1.2 to 5.9 km. Spawner densities were more variable within the longer strata examined on the Lower Shuswap River than on the Nicola River.

3.1.2.2 Scaled Spawner Density Models

The scaled spawner density biostandards for the Nicola and Lower Shuswap rivers were near the high end of the range of the spawner density biostandards for other rivers. The scaled area biostandard for the Nicola River (2.36 spawners/100 m^2) exceeded the scaled biostandard for the Lower Shuswap River (1.39 spawners/100m^2), whereas the scaled linear biostandard for the Lower Shuswap River (823 spawners/km) exceeded the scaled biostandard for the Nicola River (529 spawners/km).

3.2 Case Study Examples

3.2.1 Habitat-Based Models

3.2.1.1 Group 5 Lower Thompson

The linear and area habitat suitability model predictions exceeded the maximum escapement estimates for all systems, except Spius Creek, and few of the confidence intervals included the maximum escapement estimates (Table 6). In Spius Creek, little habitat existed within the range of gradients used by Nicola River mainstem spawners, thus the habitat suitability models were inappropriate for this system (Figure 14). The area model predictions had smaller relative deviations than the linear model, indicating more accurate predictions. For both models, there was little statistical bias in spawner capability estimates, except for Spius Creek. Estimates from the linear model were more precise than estimates from the area model because the area model was influenced by uncertainty in the estimation of wetted width. The scaled linear habitat suitability model predicted larger spawning habitat capacity than the scaled area model. The spawner capacity estimates had little statistical bias, except for Spius Creek, and estimates from the linear model were more precise than estimates from the area model.

Among the spawner density models, the linear model predictions were higher than the area model predictions, similar to the pattern observed for the habitat suitability models (Table 7). The spawner capability estimates from the area spawner density model had low statistical bias (~0%) and confidence intervals exceeded the maximum escapement estimates for all systems except Bonaparte River. Also, scaled spawner density models had higher predictions for the linear model than area model, and area model predictions had low statistical bias (~0%).

The linear and area spawner density models had generally higher predictions for most streams than the habitat suitability models, as indicated by the larger relative deviations. The spawner density models developed more appropriate estimates for Spius Creek than the habitat suitability models because predictions were based on stream length or wetted stream area and ignored habitat quality. In comparison, habitat suitability models were based on habitat quality (gradient) and a stratification system intended to develop stream groups with relatively similar habitat.

3.2.1.2 Group 4 Lower-South Thompson

Some of the linear and area habitat suitability models predictions were higher than the maximum escapement estimates whereas others were lower, and the absolute size of the relative deviations was larger than was observed for Group 5 (Table 8). The confidence intervals for the linear and area model predictions included the maximum escapement estimates for the Lower Shuswap and South Thompson rivers, but not for the other systems. Spawner capability estimates from the linear and area models had

similar precision and statistical bias. Both models had little statistical bias in spawner capability estimates, except for Lower Adams and Little rivers. In addition, the scaled linear and area habitat suitability models had similar precision and bias, which were similar to the habitat suitability models.

For the linear and area habitat suitability models, spawner capability was underestimated in Lower Adams and Little rivers. At the scale of the prediction strata there was little habitat in Lower Adams River within the range of gradients used by Lower Shuswap River spawners, thus the habitat suitability models were inappropriate for these systems. Furthermore, the gradient in much of the Little River was calculated to be negative, indicating the stream bank increased in elevation along the river's course. Little River is low gradient, flows through a terminal glacial moraine separating Shuswap and Little Shuswap lakes, and has abundant high quality spawning gravel. In contrast, spawner capacity was overestimated in the Thompson River. Unlike the Lower Adams River, most of the habitat in the Thompson was within the range of gradients used by Lower Shuswap spawners. However, the Thompson is deeply incised in the interior plateau and confined by canyons and steep banks for large distances, and little of the main channel appears suitable for spawning. Although the Thompson had low gradient, the confined channel concentrated the stream's flow and suitable gravel for spawning appears scarce. Also, the area models overestimated the area available for spawning due to the confined channel and overestimation of wetted width. Spawning in the Thompson River was observed in narrow strips of suitable habitat, often near the middle of the river.

The spawner density models may be more accurate than the habitat suitability models because the spawner density models had smaller relative deviations (Table 9). The confidence intervals for the area model included the maximum escapement estimate for the Lower Shuswap, but not for the other systems. The spawner density models generally underestimated the spawner capability of most systems, and all area model estimates had little statistical bias (~0%). Generally, the scaled spawner density model predictions had little statistical bias (~0%) and were higher than the linear predictions of spawner capacity.

4 Discussion

To estimate spawner capacity for chinook in the Fraser River watershed, we developed several models for various types of systems. These models were applied within two of eight population strata as case studies to assist with evaluating the habitat-based approach. To assess the accuracy of each model's predictions, spawner capability and capacity estimates were compared to the maximum spawner escapement estimate for each system.

The hierarchy we developed to stratify spawning systems performed well for most systems, yet large predictive errors occurred for high gradient and confined-channel systems. Accordingly, the population stratification did not account for all the variability in the spawner density-habitat relationships and additional stratification may be necessary.

Spawner density-habitat relationships were examined within nine systems, and seemed reasonable for five. Spawner densities were generally highest for gradients between 0.0015 and 0.006, however the position and width of the habitat suitability curve varied among systems. The case studies provided additional evidence that the spawner density-gradient relationship varied among systems. Some systems contained little habitat within the range of gradients used for spawning in other systems, resulting in large predictive errors. In high gradient systems, there may be fine-scale stretches of low-gradient channel types that may provide local spawning habitats (Montgomery et al. 1999) or micro-scale stretches of spawning habitats downstream of large features that dissipate stream energy, such as large boulders. Relationships were not evident for some systems because there were too few survey strata to develop a

habitat suitability curve, the survey strata were long and contained a wide range of potential spawning habitat, or there was no apparent pattern despite ample strata. Also, factors other than gradient may contribute to the variation in spawning habitat use and stream-specific phenomena may cause variability among stream-specific habitat suitability curves.

For both case studies, spawning habitat capacity was estimated from scaled habitat suitability curves, which were habitat suitability models adjusted to the maximum spawner density measured in the river. For Group 5 Lower Thompson, spawner capacity estimates always exceeded the maximum escapement estimates, indicating that the scaling factors are probably too large. At the Nicola River, spawner densities were measured in sections that were about two orders of magnitude smaller than the prediction strata. The difference in scale may have resulted in positively biased scaling factors and consequently over-estimates of spawner capacity. In comparison, the Lower Shuswap River sections were similar in length to the prediction strata, and spawner capacity estimates were within the range of the maximum escapement estimates.

The spawner density models may be better suited for developing spawner capacity estimates than the habitat suitability models. Both model types performed similarly, but the spawner density models were simpler and the estimates more precise than the habitat suitability models. When biostandards were pooled among the nine streams, the linear spawner density model had better overall fit than the habitat suitability model, whereas the area habitat suitability model had better overall fit than the area spawner density model. Among the case study examples, no individual model was consistently better than the other. For example, for Group 5 systems, the area habitat suitability model predictions had smaller relative deviations from maximum escapement estimates and appeared to perform better than the linear habitat suitability and both spawner density models. For Group 4 systems, the area spawner density model had smaller relative deviations from maximum escapement estimates and appeared to perform better than the linear spawner density and both habitat suitability models. Accordingly, several models should be evaluated when developing reference points and estimates could be combined with Bayesian, inverse variance weighting, or other methods (Hilborn and Walters 1992).

Spawning capacity estimates had high uncertainty when developed from relationships with moderate coefficients of determination. The influence of the uncertainty in the spawner density-gradient relationship was evident among comparisons of spawner capability estimated from the linear habitat suitability models between Group 4 and Group 5 systems because these models did not estimate wetted width. The lower coefficient of determination for the Lower Shuswap River relationship (0.80) than Nicola River (0.96) contributed to the larger CVs for spawner capacity estimates from the Lower Shuswap relationship than the Nicola relationship. Comparison of spawner capabilities from the linear and area models indicated that the estimation of wetted width was a minor source of variability. The $\hat{A}_{k,l}$, $\hat{M}_{k,l}$ and $\hat{S}_{k,l}$ parameters were uncorrelated for the Nicola (all R^2<0.26) and Lower Shuswap (all R^2<0.16) habitat suitability curves, accordingly the range distribution of $\hat{F}(\hat{C}^{*}_{l,n})$ should be a reasonable approximation. Structural uncertainty in the predictive relationships could be addressed from the collection of better experimental data to determine good and sub-optimal spawning habitat and assess its relationship to gradient and other potential independent variables.

Following the development of spawning capacity estimates, additional reference points can be calculated. Reference points are often expressed in terms of fish density or population abundance. The spawner abundance producing MSY (S_{MSY}) is a biologically meaningful reference point of particular relevance to the Pacific Salmon Treaty (PSC 2000). Biological risk to the population increases with decreasing abundance below this reference point. The Ricker curve adequately describes the relationship between stock and recruitment for chinook populations (CTC 1999; Schaller et al. 1999), and Hilborn (1985)

demonstrated that S_{MSY} could be approximated from the stock-recruitment curve from estimates of capacity and productivity. Measuring stock productivity requires considerable data sufficient to estimate stock-recruitment relationships, which were not available for Fraser River chinook populations, with the exception of the Harrison River (Brown et al. 2001). However, Myers et al. (1999) found that stock productivity was relatively constant within a species, accordingly values from other populations could be useful in a meta-analysis to calculate S_{MSY}. Bootstrap or Bayesian methods could be applied to incorporate uncertainty into estimates of S_{MSY} and assist fisheries managers with evaluating the risk of management options.

In sum, we described habitat-based methods to develop estimates of spawner capacity for Fraser River chinook populations. Fraser chinook spawning systems were stratified according to biophysical characteristics outlined in the classification hierarchy. Next, a representative subset of systems was examined within each strata to develop biostandards and assess spawner density-habitat relationships. Then, predictive relationships for numbers of spawners considering, and then alternatively ignoring, habitat quality were used to estimate spawner capacity. We conducted two case studies as examples of applying these habitat-based approaches to assist with their evaluation. Different reference points will need to be calculated depending on whether we are managing for production, ecosystem, social, or economic objectives. Candy et al. (2002) described provisional Conservation Units for Fraser chinook and it is necessary to define management objectives for each Conservation Unit in order to determine which reference points are needed.

5 Summary and Recommendations

- Habitat suitability and spawner density models are useful for developing estimates of spawner capacity for Fraser River chinook salmon. However, spawner density-gradient relationships vary among rivers and large errors were evident when models were applied incorrectly for some systems. Additional stratification and model development may produce more accurate estimates of spawner capacity for populations spawning in high gradient or confined-channel systems.

- Spawner capacity was sensitive to scaling factors and additional work is required to develop scaling factors that correspond with the scale of prediction strata.

- Spawning capacity estimates have high uncertainty when developed from relationships with moderate coefficients of determination. Additional work is required to establish survey strata corresponding to spawning habitat quality on more intensively monitored systems to develop more accurate and precise habitat suitability models.

- Spawning capacity estimates were generated and now, Conservation Units need to be agreed upon and management objectives defined for each Conservation Unit in order to specify which reference points are needed.

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8 Tables

Table 1. Biophysical characteristics of spawning system groups.

	Spawning System Groups							
	Large Lake Moderating Influence				Small or No Lake Moderating Influence			
Biophysical Characteristics	**Group 1 Lower Fraser**	**Group 2 Middle Fraser**	**Group 3 North Thompson**	**Group 4 Lower-South Thompson**	**Group 5 Lower Thompson**	**Group 6 Lower-Middle Fraser**	**Group 7 Upper Fraser**	**Group 8 North-South Thompson**
Watershed Area (km^2)								
Mean	8,324	10,350	12,069	20,429	3,162	2,369	977	713
Range	NA	728-51,900	4,915-20,742	3,323-55,665	780-7,227	210-12,400	100-5,550	46-387
n	1	8	3	4	5	22	29	17
MAD (m^3/s)								
Mean	482	94.4	225	311	9.36	13.7	26.5	10.9
Range	NA	16-245	34-420	74-759	2.85-22.7	2.1-64.0	3.19-209	0.90-37.7
n	1	8	3	5	5	22	29	18
Water Yield ($m^3/s*km^2$)								
Mean	0.0579	0.0152	0.0160	0.0181	0.0052	0.0106	0.0326	0.0185
Range	NA	0.0044-0.0291	0.0069-0.0209	0.0136-0.0223	0.0008-0.0120	0.0011-0.0520	0.0055-0.0418	0.0031-0.0421
n	1	8	3	4	5	22	29	17
Peak Flow Index								
Mean	2.8	3.8	4.6	3.3	7.9	6.6	6.0	7.8
Range	NA	2.3-5.3	4.4-4.9	3.0-4.2	4.6-10.0	3.5-10.1	4.4-9.4	5.0-9.9
n	1	8	3	5	5	22	29	17
Mean G7 (days)								
Mean	254	167	NA	194	177	159	110	145
Range	NA	146-194	NA	166-205	146-197	111-200	83-130	85-196
n	1	9	NA	5	3	8	4	11
Peak Spawning Week[1]								
Mean[1]	45	39	39	41	36	35	34	37
Range[1]	NA	36-43	38-39	40-42	35-37	33-44	32-36	33-40
n	1	9	3	5	5	24	35	17

1. Measured in statistical weeks where week 1 corresponds to January 1 to 7.

Table 2. Definitions of the subscripts used for model parameters.

Subscript	Description
i	Year
j	Spawner index stratum
k	Spawner index river
l	Measurement units for linear (per km) or area (per m^2) application
m	Prediction stratum
n	Prediction river
s	Scaled parameter

Table 3. Non-linear regression estimates of the mean ($\hat{M}_{k,l}$), standard deviation ($\hat{S}_{k,l}$), area-under-the-curve ($\hat{A}_{k,l}$), the coefficient of determination (R^2), ANOVA F-test results, and Kolmogorov-Smirnov one-sample test (K-S) results for habitat suitability curves.

	$\hat{M}_{k,l}$	$\hat{S}_{k,l}$	$\hat{A}_{k,l}$	R^2	ANOVA P-value	K-S P-value[1]
Linear Models						
Nicola River	$2.75*10^{-3}$	$1.06*10^{-3}$	1.35	0.99	<0.001	0.997
Lower Shuswap River	$1.67*10^{-3}$	$6.29*10^{-4}$	5.84	0.80	<0.001	0.772
Chilko River	$4.69*10^{-3}$	$1.78*10^{-3}$	10.1	0.96	<0.005	0.747
Raft River	$4.03*10^{-3}$	$1.63*10^{-3}$	8.11	0.68	<0.025	0.924
Elkin Creek	$2.10*10^{-3}$	$1.12*10^{-3}$	0.225	0.80	<0.05	0.341
Area Models						
Nicola River	$2.59*10^{-3}$	$1.16*10^{-3}$	$7.21*10^{-5}$	0.98	<0.001	0.321
Lower Shuswap River	$1.67*10^{-3}$	$6.34*10^{-4}$	$9.98*10^{-5}$	0.79	<0.001	0.792
Chilko River	$4.69*10^{-3}$	$1.78*10^{-3}$	$1.87*10^{-4}$	0.96	<0.005	0.747
Raft River	$4.03*10^{-3}$	$1.63*10^{-3}$	$3.60*10^{-4}$	0.68	<0.025	0.924
Elkin Creek	$2.12*10^{-3}$	$1.01*10^{-3}$	$2.62*10^{-5}$	0.80	<0.05	0.341

1. *P*-value for Kolmogorov-Smirnov One-Sample test for normally distributed residuals.

Table 4. Maximum escapement estimates, sum of maximum strata escapement estimates, and spawner density biostandards for spawner density models.

	Maximum Escapement		Sum of Maximum Strata Escapements	Spawner Density Biostandards ($\hat{D}_{j,k,l}$)	
River	Estimate	Year	$\sum_j \max \hat{N}_{j,k}$	Linear (spawners/km)	Area (spawners/m^2)
Chilko	17,000	1996	22,033	544.9	$1.00*10^{-2}$
Nechako	9,331	2001	9,587	50.8	$9.94*10^{-4}$
Clearwater	7,830	1997	11,683	168.2	$1.99*10^{-3}$
Mahood	700	1988	415	453.0	$1.33*10^{-2}$
Lower Shuswap	37,536	2001	37,611	518.4	$8.72*10^{-3}$
Nicola	17,777	1996	18,960	160.7	$7.20*10^{-3}$
Elkin	1,250	1996	605	79.8	$7.79*10^{-3}$
Willow	2,041	1998	2,057	50.2	$1.14*10^{-3}$
Bowron	10,900	1987	8,686	74.2	$1.60*10^{-3}$
Raft	1,371	1995	1,924	449.4	$2.00*10^{-2}$

Table 5. Spawner density and physical data used to develop scaling factors for the Nicola and Lower Shuswap rivers.

Strata	Length (m)	Wetted Area (m^2)	Spawners	Spawner Density (spawners/km)	Spawner Density (spawners/100 m^2)	Scaling Factors Linear	Scaling Factors Area
Nicola							
1	44	1460	86	1,960	5.89	3.9	2.4
2	40	1060	38	945	3.57	1.9	1.4
3	41	1170	26	639	2.22	1.3	0.9
4	31	654	26	839	3.98	1.6	1.6
5	35	374	16	452	4.28	0.9	1.7
6	38	517	32	849	6.19	1.7	2.5
7	21	295	24	1,160	8.15	2.3	3.3
Average				979	4.90	2.0	2.0
Lower Shuswap							
1	170	10,000	923	5,430	9.21	1.5	1.5
2	150	8,840	874	5,830	9.88	1.6	1.6
3	1,350	79,600	6,280	4,650	7.89	1.3	1.3
Average				5,300	8.99	1.4	1.4

Table 6. Spawner capability and capacity predictions for spawning systems in Group 5 Lower Thompson for linear and area habitat suitability and scaled habitat suitability models.

		Habitat Suitability Models					Scaled Habitat Suitability Models				
Spawning System	Maximum Escapement	Spawner Capability[1]	CV[2]	Confidence Interval	SB[3]	Relative Deviation[4]	Spawner Capacity[5]	CV[2]	Confidence Interval	SB[3]	Relative Deviation[4]
Linear											
Bonaparte	10,084	19,800	0.04	18,300-21,200	0%	+96%	76,200	0.04	70,700-81,700	0%	655%
Coldwater	3,703[7]	5,120	0.05	4,640-5,650	0%	+38%	19,700	0.05	17,900-21,800	0%	+433%
Deadman	1,591	5,290	0.04	4,860-5,760	0%	+232%	20,400	0.04	18,700-22,200	0%	1,182%
Nicola[6]	15,434[8]	17,600	0.04	16,200-18,700	0%	+13%	67,300	0.04	62,500-72,300	0%	+336%
Spius	1,269[9]	10	0.29	5-16	-4%	-99%	37	0.29	20-63	-5%	-97%
Total	32,081	47,600	0.04	44,200-51,200	0%	+49%	184,000	0.04	170,000-197,000	0%	+473%
Area											
Bonaparte	10,084	12,300	0.06	10,900-13,700	0%	+22%	40,500	0.06	35,800-45,000	0%	+301%
Coldwater	3,703[7]	3,900	0.09	3,220-4,520	0%	+4%	12,600	0.09	10,600-14,900	0%	+242%
Deadman	1,591	2,400	0.08	2,060-2,770	0%	+51%	7,890	0.08	6,760-9,090	0%	+396%
Nicola[6]	15,434[8]	17,500	0.06	15,500-19,800	0%	+14%	57,900	0.06	50,800-65,100	0%	+275%
Spius	1,269[9]	10	0.46	4-25	-6%	-99%	37	0.46	12-82	-2%	-97%
Total	32,081	36,200	0.06	31,900-45,300	0%	+13%	119,000	0.06	104,900-133,000	0%	+271%

1. Refers to the number of spawners a system would contain based on maximum observed spawner densities.
2. Coefficient of variation.
3. Statistical bias was the difference between the average of the bootstrap estimates and the point estimate expressed as a percentage of the point estimate.
4. Difference between the spawner capability (or capacity) estimate and the maximum escapement estimate expressed as a percentage of the maximum escapement estimate.
5. The spawner carrying capacity for the system.
6. Includes Nicola, Guichon, upper Nicola, and Spahomin systems.
7. Maximum escapement to upper Coldwater River (1,500) plus escapement for lower Coldwater (2,203).
8. Maximum escapement to Nicola, Spahomin, Guichon, upper Nicola, lower Coldwater, and lower Spius (17,777) minus lower Spius (140) and lower Coldwater that year.
9. Maximum escapement to upper Spius (900) plus maximum escapement for lower Spius (369).

Table 7. Spawner capability and capacity predictions for spawning systems in Group 5 Lower Thompson for linear and area spawner and scaled spawner density models.

	Spawner Density Models				Scaled Spawner Density Models			
Spawning System	**Spawner Capability[2]**	**CV[3]**	**Confidence Interval**	**Relative Deviation[4]**	**Spawner Capacity[5]**	**CV[3]**	**Confidence Interval**	**Relative Deviation[4]**
Linear								
Bonaparte	18,900	NA[1]	NA[1]	+87%	62,000	NA[1]	NA[1]	+515%
Coldwater	13,000	NA[1]	NA[1]	+251%	42,700	NA[1]	NA[1]	+1,050%
Deadman	8,140	NA[1]	NA[1]	+412%	26,700	NA[1]	NA[1]	+1,580%
Nicola[6]	25,900	NA[1]	NA[1]	+68%	85,000	NA[1]	NA[1]	+450%
Spius	7,700	NA[1]	NA[1]	+507%	25,300	NA[1]	NA[1]	+1,890%
Total	73,600	NA[1]	NA[1]	+129%	242,000	NA[1]	NA[1]	+654%
Area								
Bonaparte	10,100	0.01	9,860-10,300	0%	33,100	0.01	32,400-33,800	+228%
Coldwater	9,000	0.01	8,770-9,240	+143%	29,600	0.01	28,800-30,400	+699%
Deadman	3,420	0.02	3,300-3,530	+115%	11,200	0.02	10,900-11,600	+606%
Nicola[6]	19,600	0.01	19,200-20,000	+27%	64,400	0.01	63,100-65,800	+317%
Spius	6,010	0.02	5,810-6,220	+374%	19,800	0.02	19,000-20,400	+1,460%
Total	48,100	0.01	47,600-48,700	+50%	158,000	0.01	156,000-160,000	+393%

1. NA indicates there was no estimate because bootstrap analyses were not performed.
2. Refers to the number of spawners a system would contain based on maximum observed spawner densities.
3. Coefficient of variation.
4. Difference between the spawner capability (or capacity) estimate and the maximum escapement estimate expressed as a percentage of the maximum escapement estimate.
5. The spawner carrying capacity for the system.
6. Includes Nicola, Guichon, upper Nicola, and Spahomin systems.

Table 8. Spawner capability and capacity predictions for spawning systems in Group 4 Lower-South Thompson for linear and area habitat suitability and scaled habitat suitability models.

Spawning System	Maximum Escapement	Habitat Suitability Models: Spawner Capability[1]	CV[2]	Confidence Interval	SB[3]	Relative Deviation[4]	Scaled Habitat Suitability Models: Spawner Capacity[5]	CV[2]	Confidence Interval	SB[3]	Relative Deviation[4]
Linear											
Middle Shuswap	5,000	25,000	0.16	17,200-33,600	+1%	+401%	39,700	0.16	27,200-53,200	+1%	+694%
Little	12,004	963	0.67	88-2,800	+12%	-92%	1,570	0.67	139-4,440	+12%	-87%
Lower Adams	7,329	72	1.36	0-720	+99%	-99%	105	1.36	0-1,140	+100%	-98%
Lower Shuswap	37,536	49,400	0.23	31,000-76,400	+3%	+32%	78,700	0.23	49,100-121,000	+3%	+110%
South Thompson[6]	41,277	28,300	0.44	10,700-61,400	+6%	-31%	45,600	0.44	16,800-97,200	+6%	+10%
Thompson	6,904	178,600	0.17	120,000-239,000	-1%	+2,490%	284,000	0.17	190,000-378,000	-1%	+3,400%
Total	110,050	645,000	0.18	187,000-396,000	+1%	+157%	448,000	0.18	296,000-626,000	+1%	+307%
Area											
Middle Shuswap	5,000	10,700	0.17	7,330-14,500	+1%	+113%	16,900	0.17	11,600-23,000	+1%	+239%
Little	12,004	1,840	0.67	173-5,390	+11%	-85%	2,930	0.67	275-8,550	+11%	-76%
Lower Adams	7,329	66	1.36	0-658	+99%	-99%	105	1.36	0-1,040	+100%	-99%
Lower Shuswap	37,536	50,400	0.23	31,900-79,100	+3%	+34%	80,000	0.23	50,700-125,000	+3%	+113%
South Thompson[6]	41,277	59,200	0.44	21,700-130,000	+6%	+43%	93,900	0.44	34,400-206,000	+6%	+127%
Thompson	6,904	523,000	0.17	356,000-703,000	-1%	+7,470%	829,000	0.17	564,000-1,120,000	-1%	+11,900%
Total	110,050	645,000	0.18	437,000-888,000	+1%	+486%	1,020,000	0.18	694,000-1,410,000	+1%	+830%

1. Refers to the number of spawners a system would contain based on maximum observed spawner densities.
2. Coefficient of variation.
3. Statistical bias was the difference between the average of the bootstrap estimates and the point estimate expressed as a percentage of the point estimate.
4. Difference between the spawner capability (or capacity) estimate and the maximum escapement estimate expressed as a percentage of the maximum escapement estimate.
5. The spawner carrying capacity for the system.
6. Includes the Thompson River from Kamloops Lake upstream to the confluence of the North and South Thompson rivers.

Table 9. Spawner capability and capacity predictions for spawning systems in Group 4 Lower-South Thompson for linear and area spawner and scaled spawner density models.

	Spawner Density Models				Scaled Spawner Density Models			
Spawning System	Spawner Capability[2]	CV[3]	Confidence Interval	Relative Deviation[4]	Spawner Capacity[5]	CV[3]	Confidence Interval	Relative Deviation[4]
Linear								
Middle Shuswap	11,300	NA[1]	NA[1]	+126%	17,900	NA[1]	NA[1]	+259%
Little	1,930	NA[1]	NA[1]	-84%	3,070	NA[1]	NA[1]	-74%
Lower Adams	6,020	NA[1]	NA[1]	-18%	9,550	NA[1]	NA[1]	+30%
Lower Shuswap	36,800	NA[1]	NA[1]	-2%	58,500	NA[1]	NA[1]	+56%
South Thompson[6]	37,300	NA[1]	NA[1]	-10%	59,200	NA[1]	NA[1]	+43%
Thompson	61,600	NA[1]	NA[1]	+792%	97,700	NA[1]	NA[1]	+1,320%
Total	155,000	NA[1]	NA[1]	+41%	246,000	NA[1]	NA[1]	+123%
Area								
Middle Shuswap	4,730	0.03	4,500-4,980	-5%	7,500	0.03	7,130-7,890	+50%
Little	3,550	0.06	3,150-3,980	-70%	5,640	0.06	5,000-6,320	-53%
Lower Adams	5,200	0.03	4,880-5,600	-29%	8,250	0.03	7,740-8,880	+13%
Lower Shuswap	37,100	0.01	36,100-38,200	-1%	58,900	0.01	57,200-60,600	+57%
South Thompson[6]	75,900	0.01	73,700-78,000	+84%	120,000	0.01	117,000-124,000	+192%
Thompson	178,000	0.01	174,000-182,000	+2,480%	283,000	0.01	277,000-289,000	+4,000%
Total	305,000	0.01	300,000-309,000	177%	484,000	0.01	476,000-491,000	+339%

1. NA indicates there was no estimate because bootstrap analyses were not performed.
2. Refers to the number of spawners a system would contain based on maximum observed spawner densities.
3. Coefficient of variation.
4. Difference between the spawner capability (or capacity) estimate and the maximum escapement estimate expressed as a percentage of the maximum escapement estimate.
5. The spawner carrying capacity for the system.
6. Includes the Thompson River from Kamloops Lake upstream to the confluence of the North and South Thompson rivers.

9 Figures

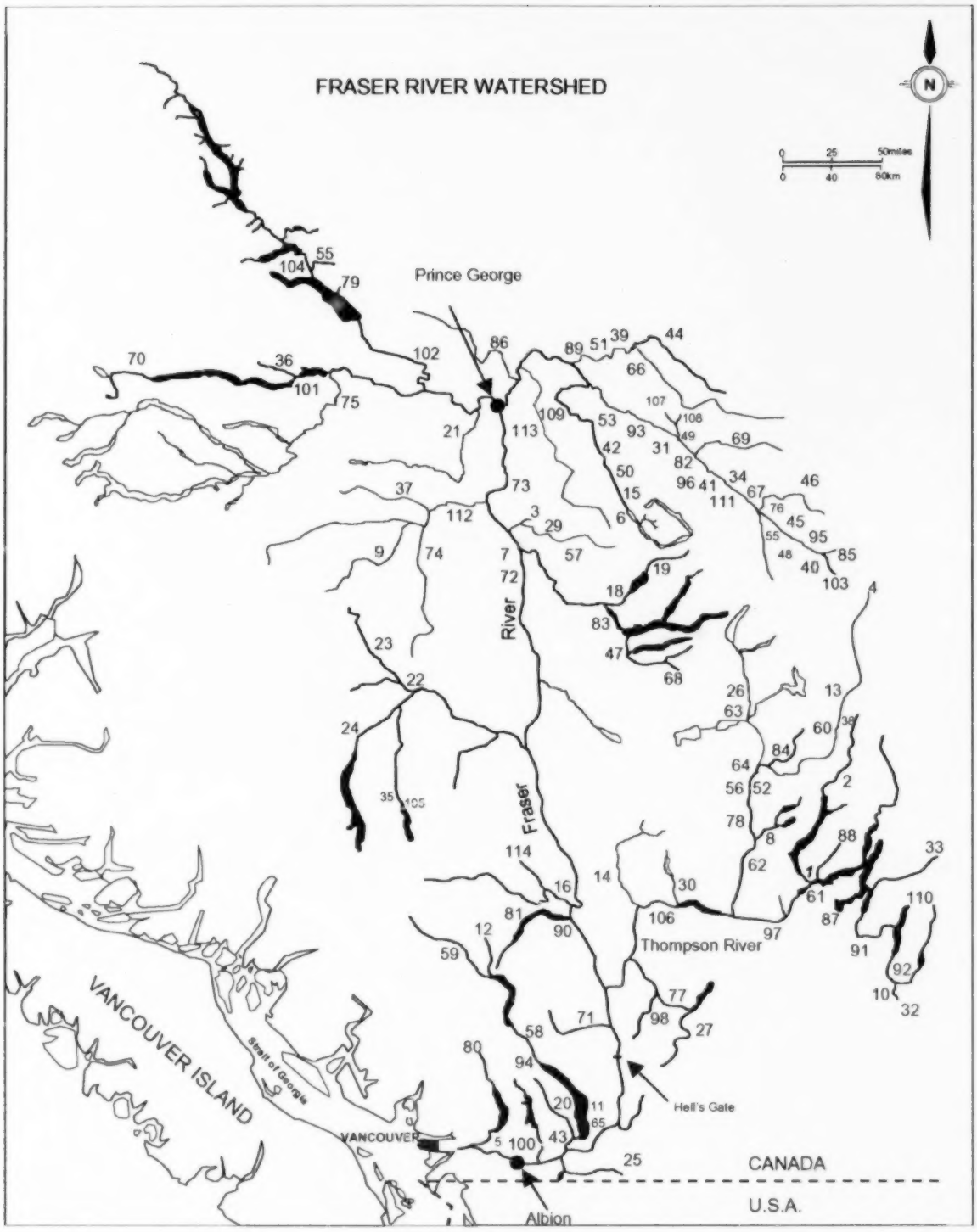


Figure 1. Chinook salmon spawning systems in the Fraser River watershed. Numbers correspond to spawning systems identified in Appendix 1.

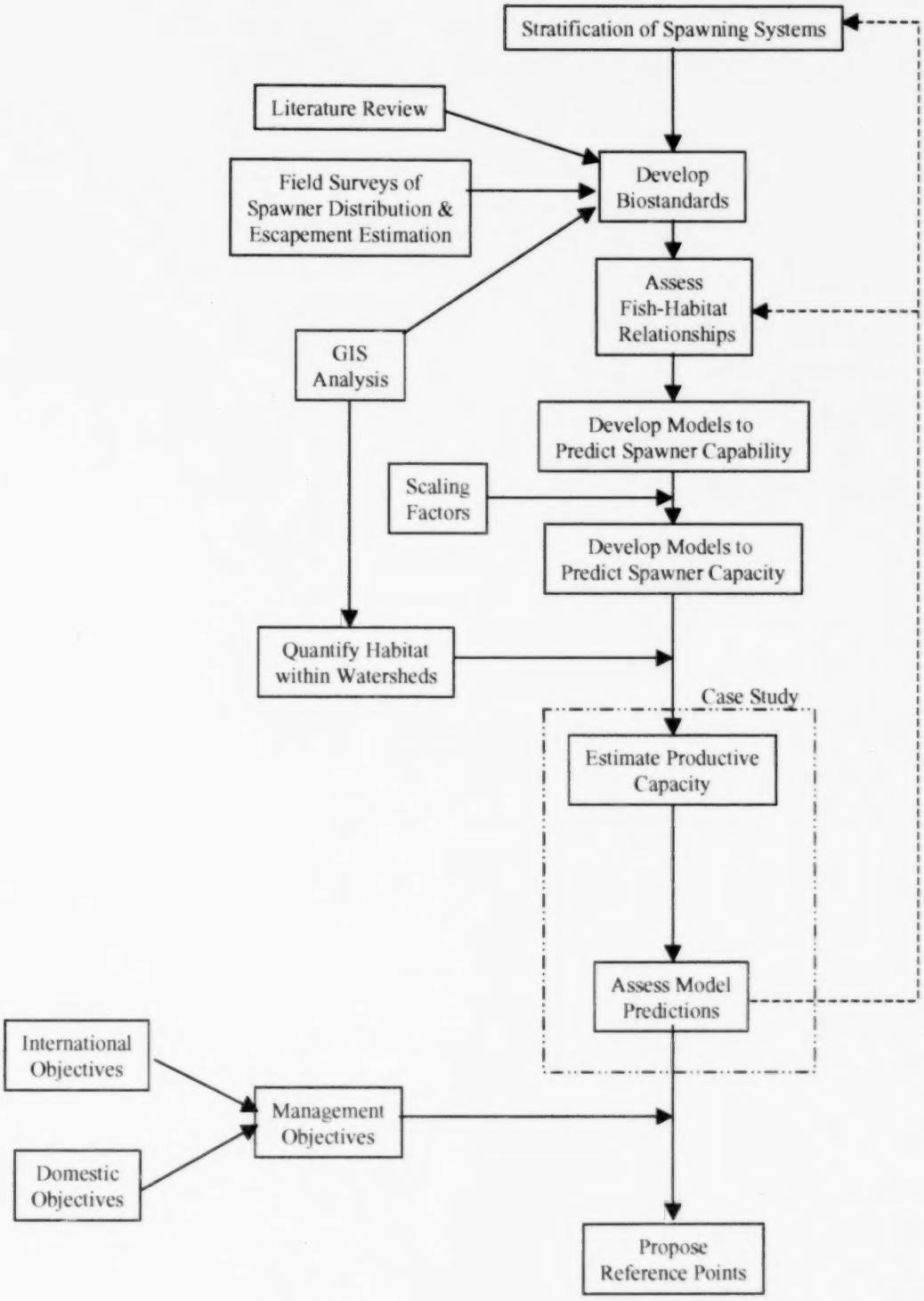


Figure 2. Overview of the steps for generating reference points for Fraser River chinook populations.

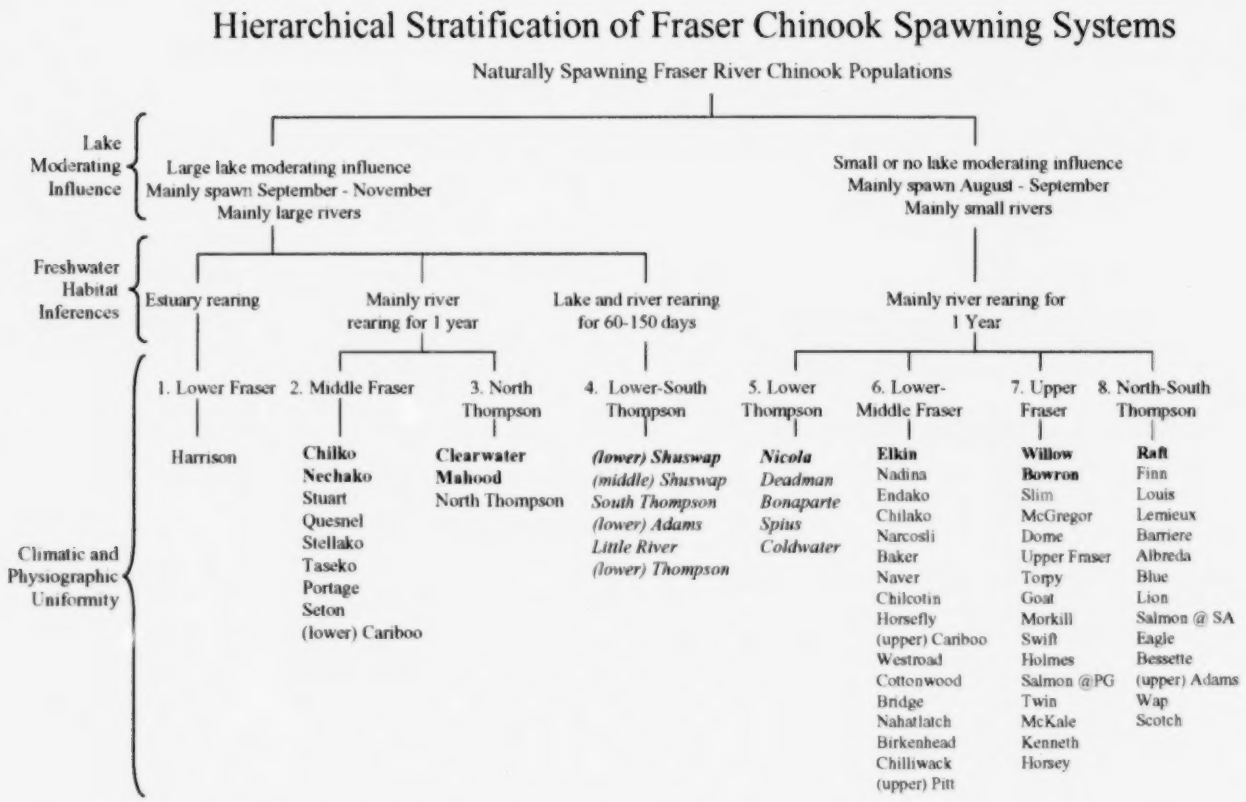


Figure 3. Hierarchical stratification of spawning systems in the Fraser River based on biophysical characteristics. Systems in bold text were chosen to investigate spawner density-habitat relationships and systems in italics were case studies.

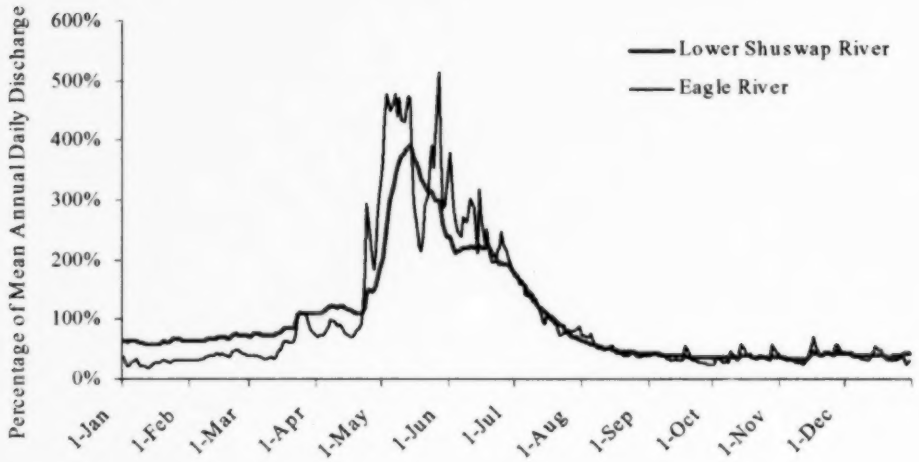


Figure 4. Percentage of mean daily discharge measured at the Eagle (non-lake moderated) and Lower Shuswap (large lake-moderated) rivers, 1998.

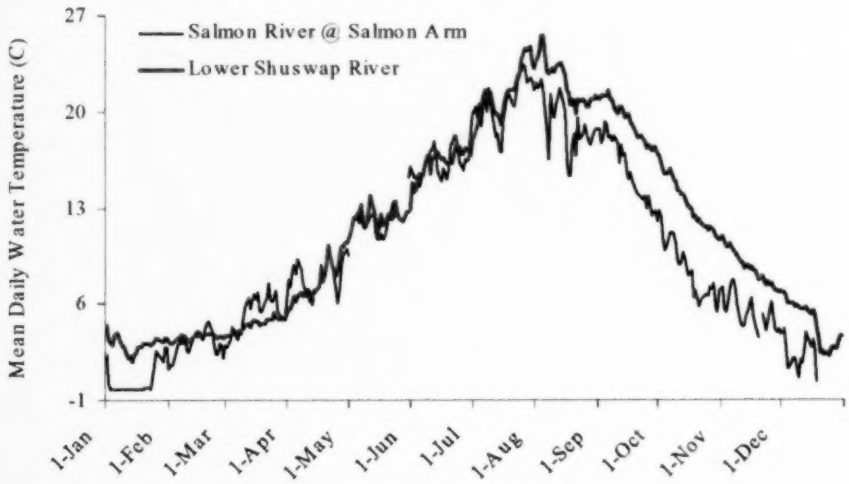


Figure 5. Mean daily water temperatures measured at the Salmon River (non-lake moderated) near Salmon Arm, BC and Lower Shuswap River (large lake-moderated), 1998.

Linear Model

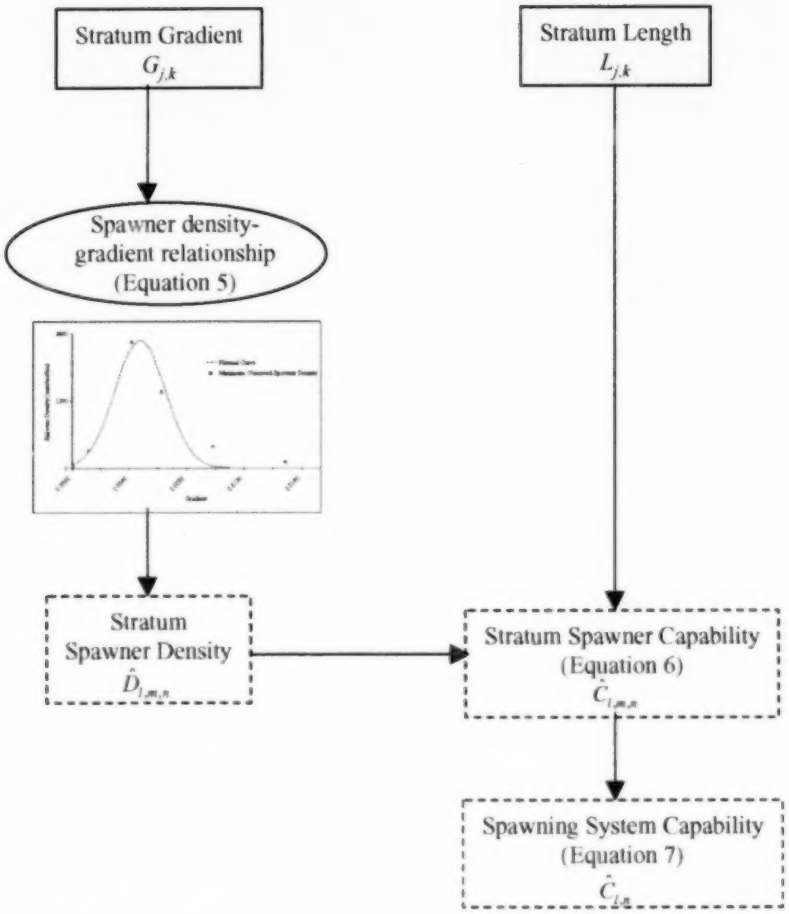


Figure 6. Flow diagram of steps in the linear habitat suitability model illustrating data variables (solid boxes), the predictive relationship (solid oval), and estimated parameters (dashed boxes).

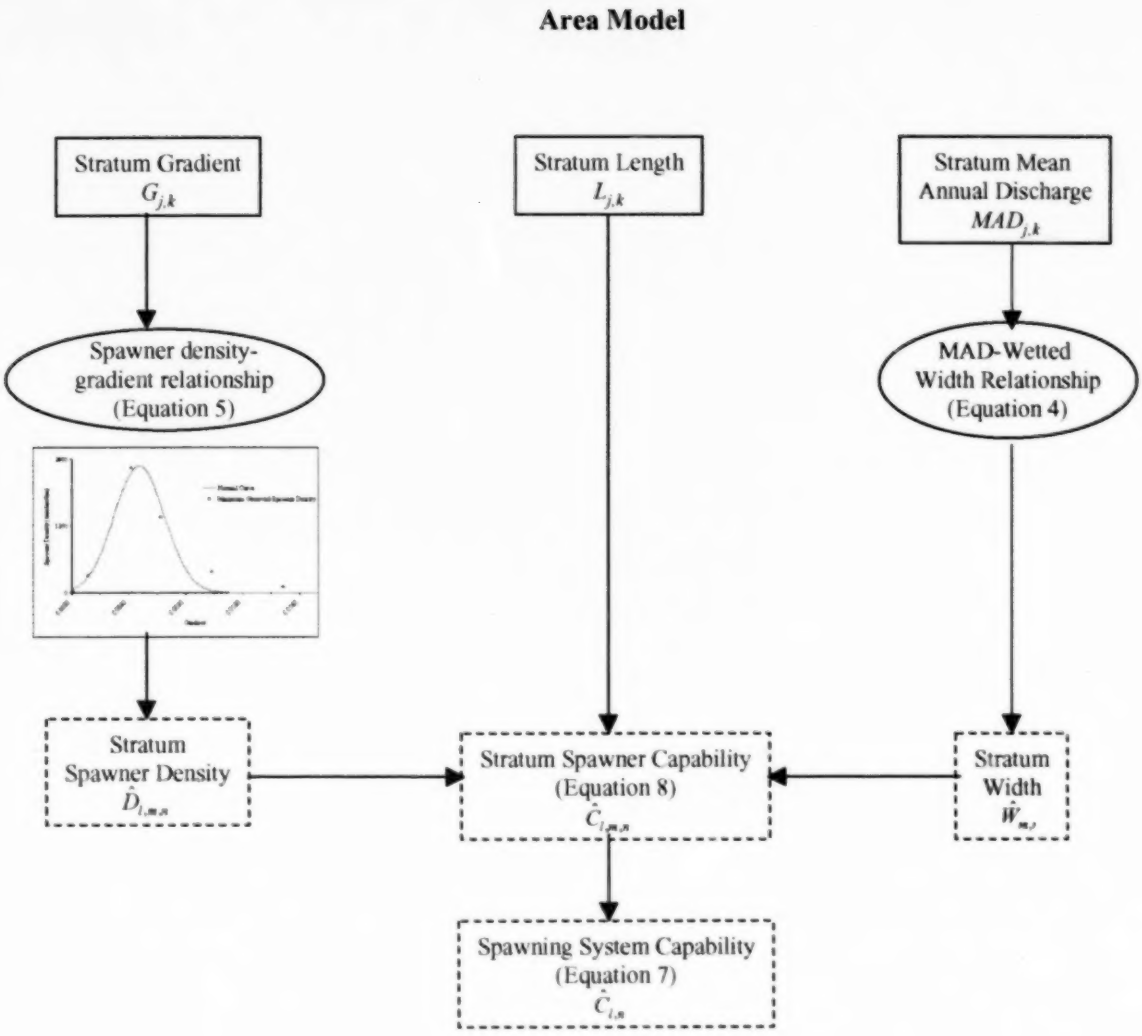


Figure 7. Flow diagram of steps in the area habitat suitability model illustrating data variables (solid boxes), predictive relationships (solid oval), and estimated parameters (dashed boxes).

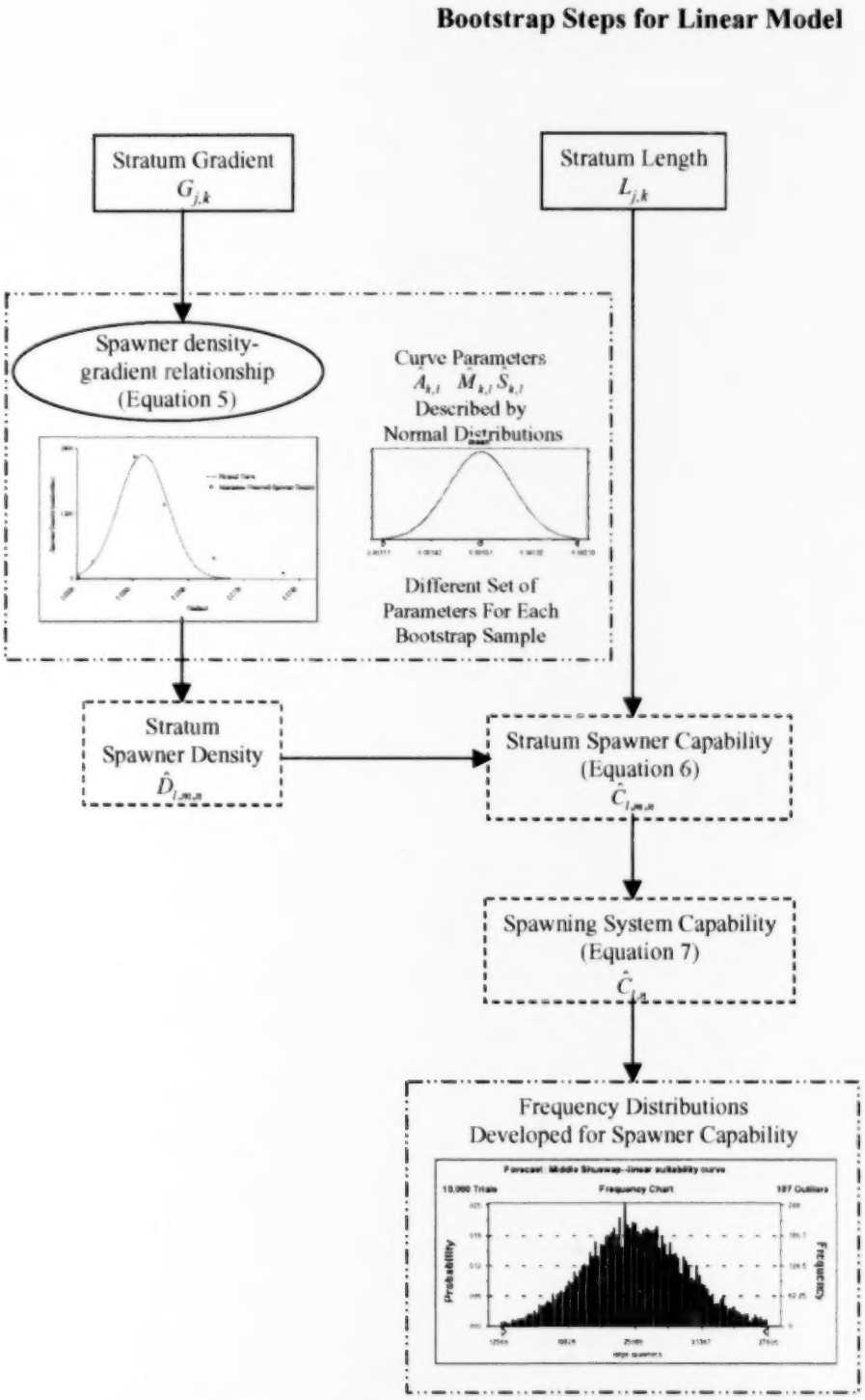


Figure 8. Flow diagram of steps in the linear habitat suitability model illustrating data variables (solid boxes), the predictive relationship (solid oval), estimated parameters (dashed boxes) and bootstrap components (large-dashed boxes).

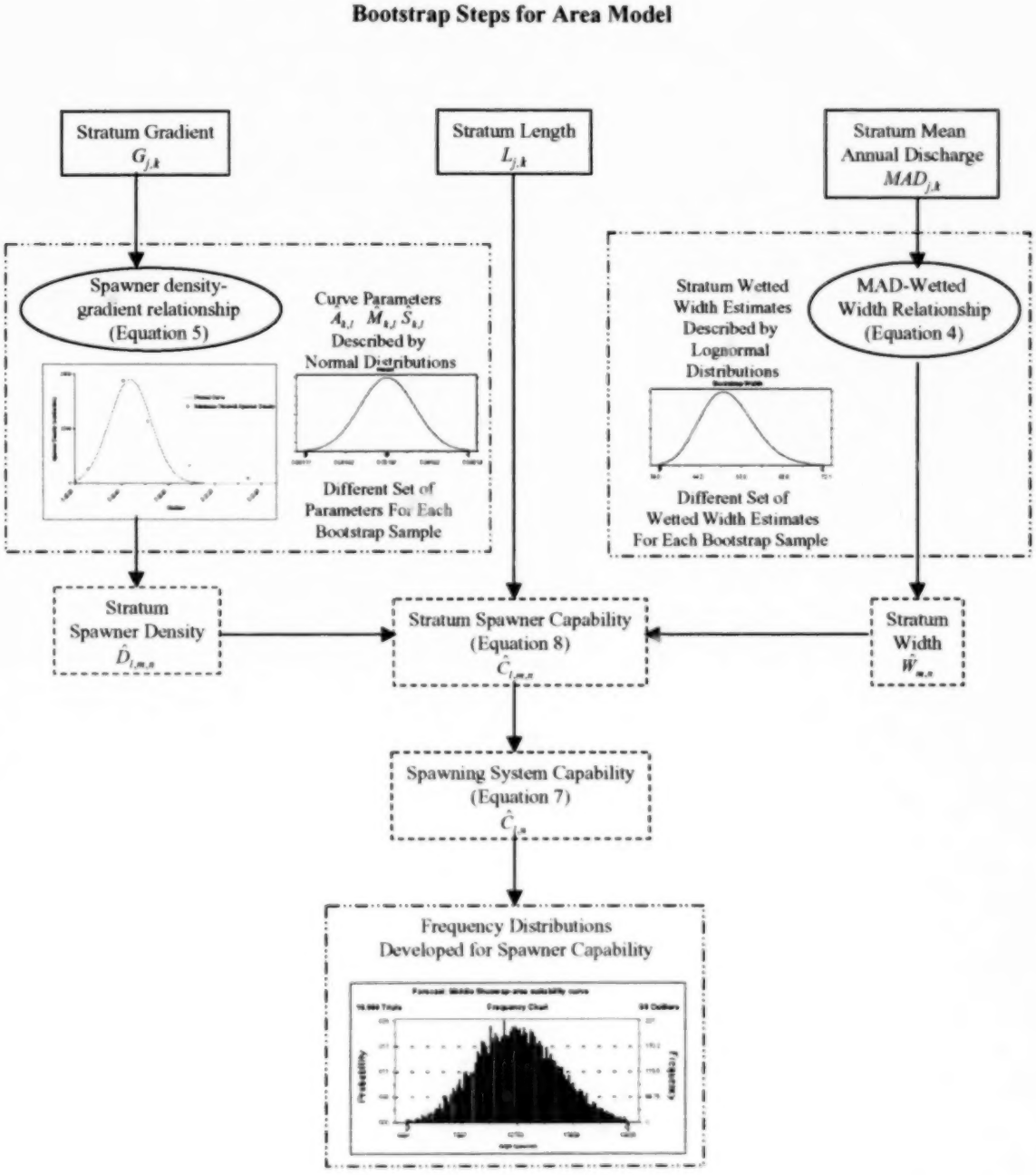


Figure 9. Flow diagram of steps in the linear habitat suitability model illustrating data variables (solid boxes), predictive relationships (solid oval), estimated parameters (dashed boxes) and bootstrap components (large-dashed boxes).

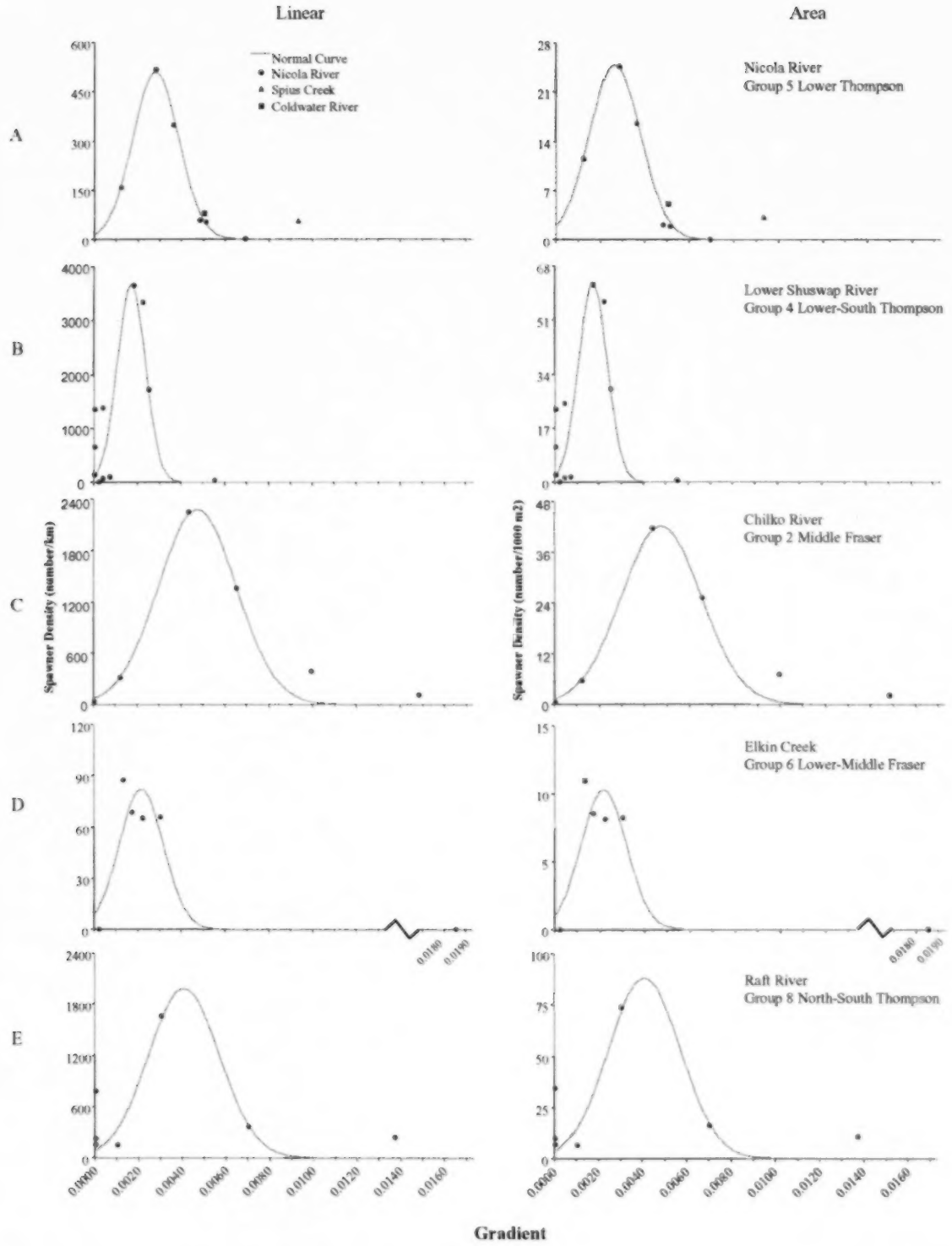


Figure 10. Habitat suitability curves describing the spawner density-gradient relationship for Nicola (A), Lower Shuswap (B), Chilko (C), and Raft (E) rivers, and Elkin Creek (D).

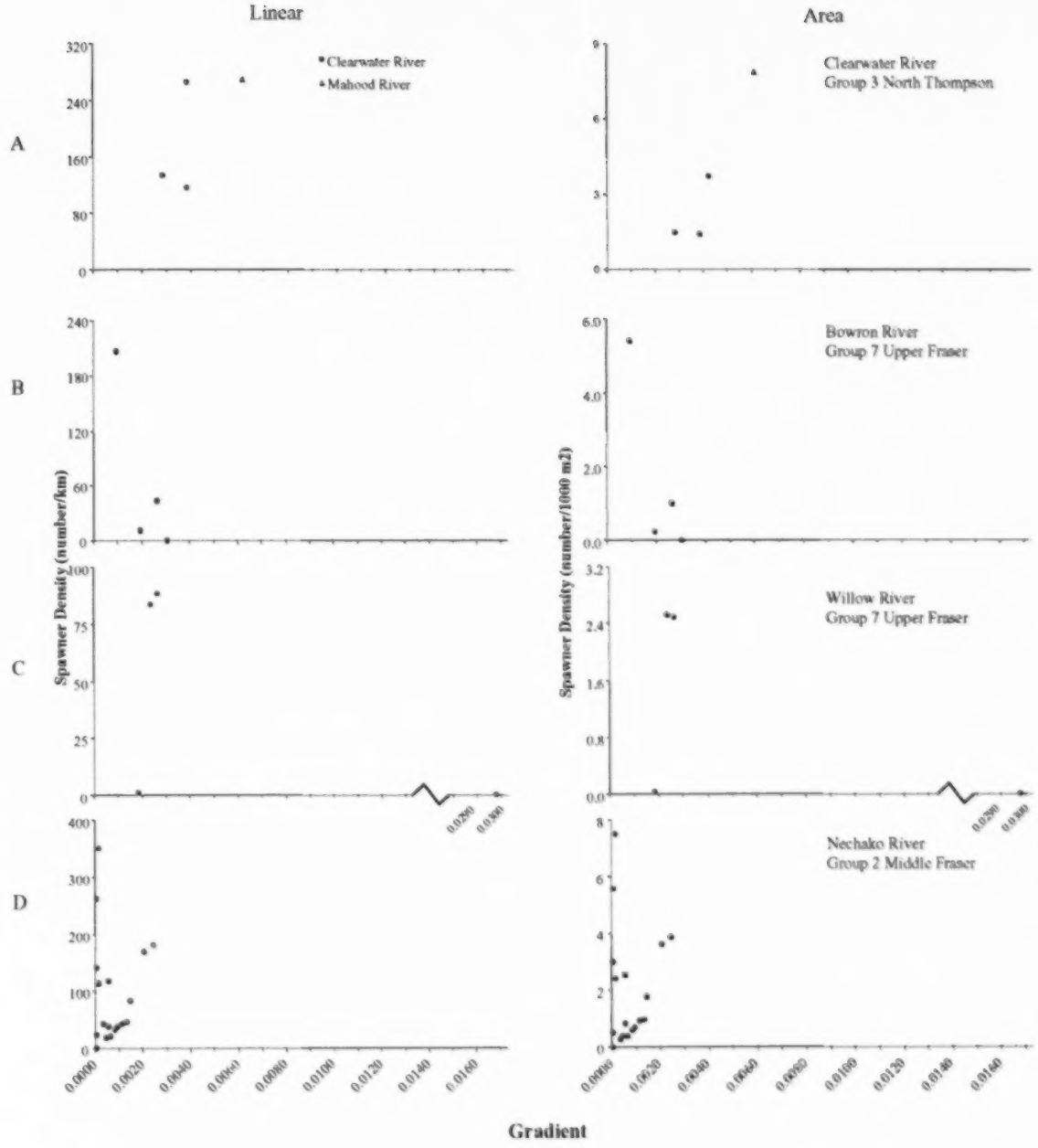


Figure 11. Scatterplots of spawner density and gradient for Clearwater (A), Bowron (B), Willow (C), and Nechako (D) rivers. No apparent relationships were seen in these systems.

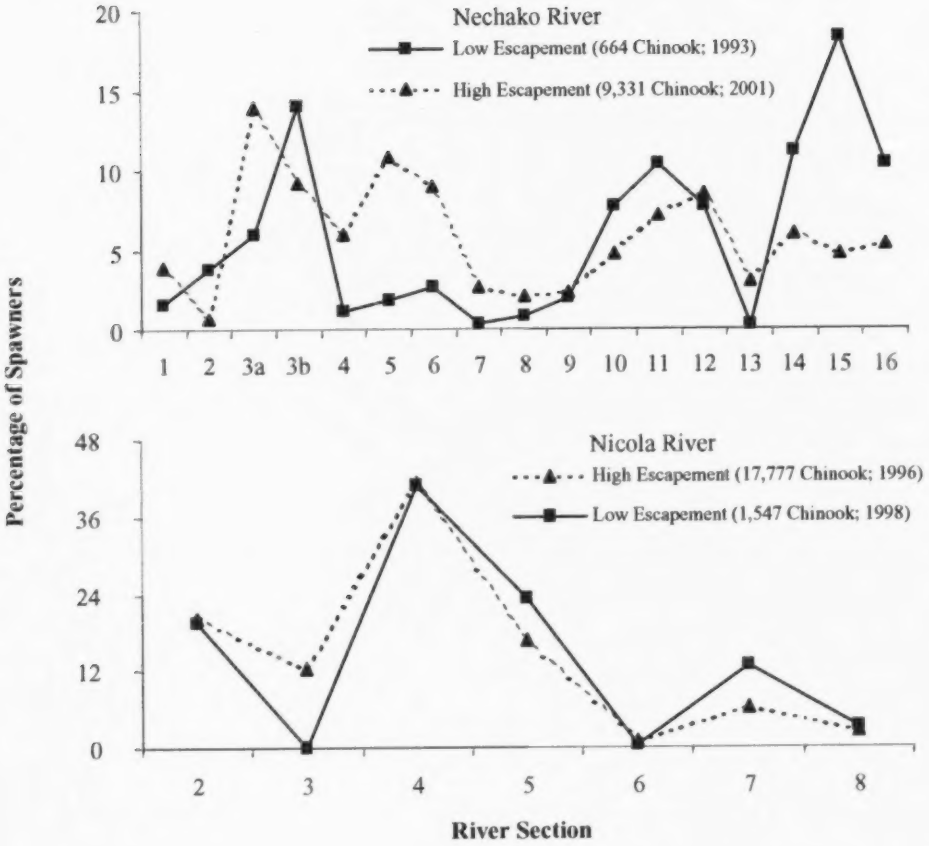


Figure 12. The relative distribution of chinook spawners in high and low escapement years for the Nechako and Nicola rivers.

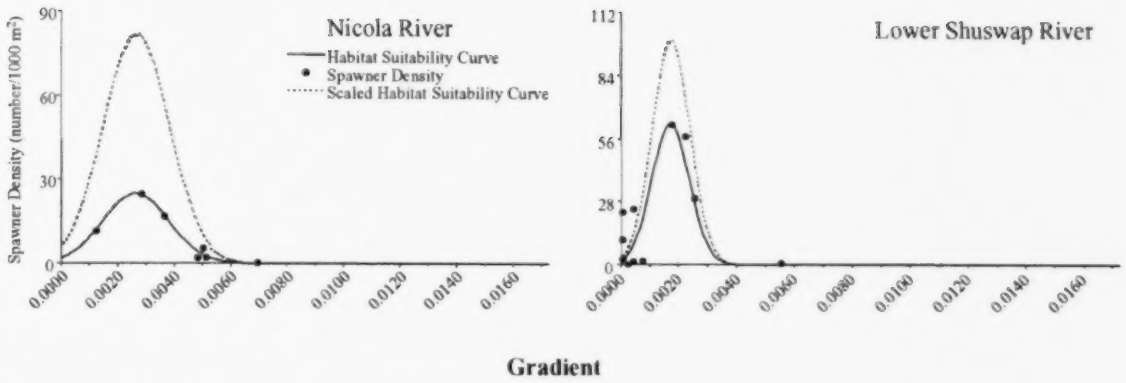


Figure 13. Scaled habitat suitability curves for Nicola and Lower Shuswap rivers.

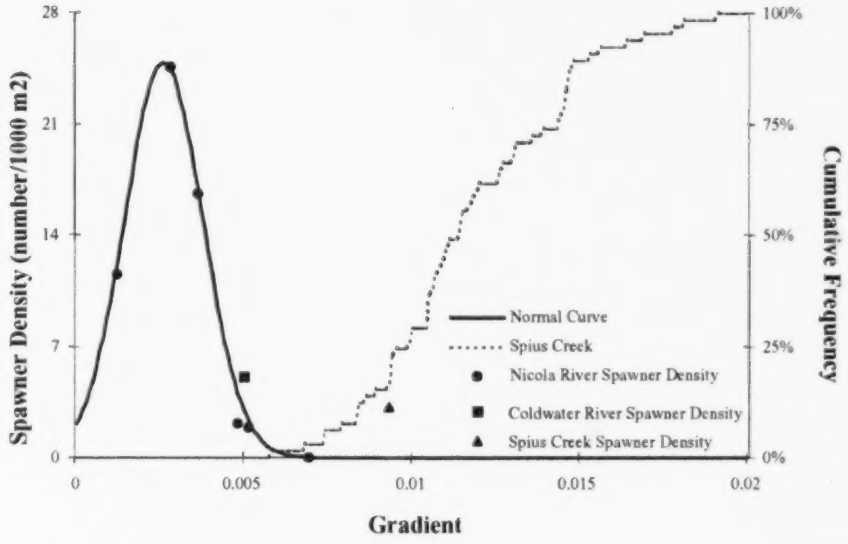


Figure 14. Habitat suitability curve fit to Nicola and Coldwater River spawner densities and the cumulative frequency distribution of potential spawning habitat by gradient in Spius Creek.

10 Appendices

Appendix 1. Biophysical characteristics of spawning systems used by chinook salmon in the Fraser River watershed.

Stream Name	Number	Basin Area (km^2)	MAD (m^3/s)	Peak Flow Index	Record Period (years)	Mean G7 (days)	Juvenile Life History[1]	Peak Spawning (week)	Most Common Age at Return[1]	Biophysical Grouping
Adams River (lower)	1	3323	74.1	3.10	80-89	166.0	ocean	10/2-10/9	4	Group 4 Lower-South Thompson
Adams River (upper)	2	3087	33.3	NA	NA	126.0	NA	9/20-9/27	NA	Group 5 North-South Thompson
Ahbau Creek	3	505	3	9.10	81-90	NA	***stream***	8/21-8/28	**5**	Group 6 Lower-Middle Fraser
Albreda River	4	406	14.3	8.29	80-89	107.7	stream	8/20-8/27	5	Group 5 North-South Thompson
Alouette River	5	332	8.07	10.46	81-90	NA	NA	NA	NA	Group 6 Lower-Middle Fraser
Antler Creek	6	359	7.34	4.42	81-90	NA	stream	8/24-8/31	5	Group 7 Upper Fraser
Baker Creek	7	1570	3.7	7.51	81-90	NA	***stream***	8/25-9/1	**5**	Group 6 Lower-Middle Fraser
Barriere River	8	1151	14.1	6.73	80-89	134.5	***stream***	9/12-9/19	**5**	Group 5 North-South Thompson
Bazeko River	9	1980	3.9	3.72	81-90	NA	***stream***	8/26-9/2	5	Group 6 Lower-Middle Fraser
Bessette Creek	10	795	4.5	7.62	80-89	166.5	stream	9/23-9/30	4	Group 5 North-South Thompson
Big Silver Creek	11	495	14.98	7.29	81-90	156.0	NA	NA	NA	Group 6 Lower-Middle Fraser
Birkenhead River	12	593	22.5	7.56	81-90	159.1	stream	9/9-9/16	5	Group 6 Lower-Middle Fraser
Blue River	13	275	9.7	8.28	80-89	NA	stream	8/25-9/1	5	Group 5 North-South Thompson
Bonaparte River	14	5390	4.51	4.61	80-89	189.0	stream	9/5-9/12	4	Group 5 Lower Thompson
Bowron River	15	3600	63.4	5.54	81-90	NA	stream	8/24-8/31	5	Group 7 Upper Fraser
Bridge River	16	4637	6.025	5.11	81-90	NA	stream	8/24-8/31	4	Group 6 Lower-Middle Fraser
Captain Creek	17	135	5.64	5.43	81-90	NA	stream	8/15-8/22	5	Group 7 Upper Fraser
Cariboo River (lower)	18	3253	94.5	4.46	81-90	156.0	stream	9/18-9/25	5	Group 2 Middle Fraser
Cariboo River (upper)	19	NA	NA	NA	NA	NA	stream	8/11-8/18	5	Group 6 Lower-Middle Fraser
Chehalis River	20	392	36.2	9.59	81-90	184.0	NA	NA	NA	Group 6 Lower-Middle Fraser
Chilako River	21	3578	12.3	6.52	81-90	NA	***stream***	8/19-8/26	**5**	Group 6 Lower-Middle Fraser
Chilcotin River (lower)	22	6220	14.8	3.51	81-90	157.5	stream	8/30-9/6	5	Group 6 Lower-Middle Fraser
Chilcotin River (upper)	23	NA	NA	NA	NA	NA	***stream***	8/14-8/21	**5**	Group 6 Lower-Middle Fraser
Chilko River	24	6940	81.5	3.52	81-90	145.8	stream	9/8-9/15	5	Group 2 Middle Fraser
Chilliwack River	25	1230	64	4.89	81-90	200.4	NA	NA	NA	Group 6 Lower-Middle Fraser
Clearwater River	26	10551	220	4.39	81-90	NA	stream	9/25-10/2	5	Group 3 North Thompson
Coldwater River	27	915	7.42	10.01	80-89	NA	stream	8/27-9/3	4	Group 5 Lower Thompson
Cottonwood River	29	2460	26	9.00	81-90	NA	stream	8/21-8/28	5	Group 6 Lower-Middle Fraser
Deadman River	30	1497	2.85	8.42	80-89	197.0	stream	9/9-9/16	4	Group 5 Lower Thompson
Dome Creek	31	273	11.4	5.43	81-90	NA	stream	8/12-8/19	5	Group 7 Upper Fraser
Duteau Creek	32	217	1.2	9.17	80-89	NA	stream	9/23-9/30	4	Group 5 North-South Thompson

Stream Name	Number	Basin Area (km^2)	MAD (m^3/s)	Peak Flow Index	Record Period (years)	Mean G7 (days)	Juvenile Life History[1]	Peak Spawning (week)	Most Common Age at Return[1]	Biophysical Grouping
Eagle River	33	1246	37.7	6.26	80-89	176.5	stream	9/14-9/21	5	Group 5 North-South Thompson
East Twin Creek	34	128	5.35	5.42	81-90	NA	***stream***	8/10-8/17	***5***	Group 7 Upper Fraser
Elkin Creek	35	210	2.1	6.19	81-90	179.0	stream	9/8-9/15	5	Group 6 Lower-Middle Fraser
Endako River	36	2033	6.13	7.03	81-90	160.0	***stream***	8/28-9/4	***5***	Group 6 Lower-Middle Fraser
Euchiniko River	37	1370	5	6.48	81-91	NA	***stream***	8/26-9/2	***5***	Group 6 Lower-Middle Fraser
Finn Creek	38	134	4.7	8.32	80-89	98.3	stream	8/10-8/17	5	Group 5 North-South Thompson
Fontiniko Creek	39	321	13.4	5.43	81-90	NA	stream	8/15-8/22	5	Group 7 Upper Fraser
Fraser River (Tete Jaune)	40	NA	NA	NA	NA	NA	stream	8/31-9/7	5	Group 7 Upper Fraser
Goat River	41	661	27.6	5.43	81-90	NA	***stream***	8/17-8/24	***5***	Group 7 Upper Fraser
Haggen Creek	42	649	13.3	4.41	81-91	NA	stream	8/24-8/31	5	Group 7 Upper Fraser
Harrison River	43	8324	481.6	2.79	81-90	254.2	ocean	11/6-11/12	4	Group 1 Lower Fraser
Herrick Creek	44	2058	86	5.43	81-90	NA	stream	8/15-8/22	5	Group 7 Upper Fraser
Holliday Creek	45	NA	NA	NA	NA	NA	***stream***	8/18-8/25	***5***	Group 7 Upper Fraser
Holmes River	46	785	32.8	5.43	81-90	115.7	stream	8/20-8/27	5	Group 7 Upper Fraser
Horsefly River	47	2860	33.2	5.51	81-90	151.0	stream	8/29-9/5	5	Group 6 Lower-Middle Fraser
Horsey Creek	48	201	8.4	5.43	81-90	NA	stream	8/23-8/30	5	Group 7 Upper Fraser
Humbug Creek	49	NA	NA	NA	NA	NA	***stream***	8/15-8/22	***5***	Group 7 Upper Fraser
Indian Point Creek	50	396	8.09	4.43	81-91	NA	stream	8/24-8/31	5	Group 7 Upper Fraser
James Creek	51	116	4.85	5.42	81-90	NA	***stream***	8/15-8/22	***5***	Group 7 Upper Fraser
Joseph	52	259	6.4	8.34	80-89	85.0	***stream***	NA	***5***	Group 5 North-South Thompson
Kenneth Creek	53	216	3.31	9.40	81-90	NA	stream	8/18-8/25	5	Group 7 Upper Fraser
Kiwa Creek	54	NA	NA	NA	NA	NA	***stream***	8/20-8/27	***5***	Group 7 Upper Fraser
Kuzkwa River	55	NA	NA	NA	NA	NA	stream	9/2-9/9	5	Group 6 Lower-Middle Fraser
Lemieux Creek	56	454	2.9	7.62	80-89	195.0	stream	10/3-10/10	4	Group 5 North-South Thompson
Lightning Creek	57	243	5	9.98	81-90	NA	***stream***	8/21-8/28	***5***	Group 6 Lower-Middle Fraser
Lillooet River (lower)	58	6109	303.05	4.48	81-90	NA	NA	NA	NA	Group 2 Middle Fraser
Lillooet River (upper)	59	3675	182.3	4.96	81-90	NA	NA	NA	NA	Group 6 Lower-Middle Fraser
Lion Creek	60	46	0.9	9.56	81-90	NA	***stream***	8/17-8/24	***5***	Group 5 North-South Thompson
Little River	61	NA	311	2.99	80-89	201.0	ocean	10/15-10/22	4	Group 4 Lower-South Thompson
Louis Creek	62	526	2.7	8.67	80-89	NA	stream	8/25-9/1	4	Group 5 Lower Thompson
Mahood River	63	4915	33.7	4.93	80-89	NA	***stream***	9/25-10/2	***5***	Group 3 North Thompson
Mann Creek	64	295	3	9.93	80-89	NA	***stream***	9/11-918	***5***	Group 5 North-South Thompson
Maria Slough	65	33	1.59	19.18	81-90	NA	ocean	10/7	4	Group 6 Lower-Middle Fraser

Stream Name	Number	Basin Area (km^2)	MAD (m^3/s)	Peak Flow Index	Record Period (years)	Mean G7 (days)	Juvenile Life History[1]	Peak Spawning (week)	Most Common Age at Return[1]	Biophysical Grouping
McGregor River	66	5550	209	5.39	81-90	83.0	***stream***	8/15-8/22	***5***	Group 7 Upper Fraser
McKale River	67	280	8.38	8.13	81-90	NA	stream	8/10-8/17	5	Group 7 Upper Fraser
McKinley Creek	68	450	5.1	5.53	81-90	NA	stream	8/29-9/5	5	Group 6 Lower-Middle Fraser
Morkill River	69	1333	55.7	5.43	81-90	111.5	***stream***	8/25-9/1	***5***	Group 7 Upper Fraser
Nadina River	70	1093	8.27	10.13	81-90	154.4	***stream***	NA	***5***	Group 6 Lower-Middle Fraser
Nahatlatch River	71	1256	38.02	6.05	81-90	111.0	stream	8/24-8/31	5	Group 6 Lower-Middle Fraser
Narcosli Creek	72	1700	3.3	8.48	81-90	NA	***stream***	8/22-8/29	***5***	Group 6 Lower-Middle Fraser
Naver Creek	73	900	6.4	7.52	81-90	NA	***stream***	8/19-8/26	***5***	Group 6 Lower-Middle Fraser
Nazko River	74	4150	4.4	6.41	81-91	NA	***stream***	8/26-9/2	***5***	Group 6 Lower-Middle Fraser
Nechako River	75	51900	244.65	2.30	81-90	172.2	stream	9/11-9/18	5	Group 2 Middle Fraser
Nevin Creek	76	137	5.73	5.43	81-90	NA	***stream***	8/8-8/15	***5***	Group 7 Upper Fraser
Nicola River	77	7227	22.7	7.93	80-89	NA	stream	9/11-9/18	4	Group 5 Lower Thompson
North Thompson River	78	20742	420	4.50	80-89	NA	stream	9/12-9/19	5	Group 3 North Thompson
Pinchi Creek	79	NA	NA	NA	NA	NA	***stream***	NA	***5***	Group 6 Lower-Middle Fraser
Pitt River	80	1660	185	13.28	81-90	NA	stream	late Aug/Sep	5	Group 6 Lower-Middle Fraser
Portage Creek	81	728	17.5	4.21	81-90	194.0	stream	10/19-10/26	5	Group 2 Middle Fraser
Ptarmigan Creek	82	183	7.65	5.42	81-90	NA	stream	8/12-8/19	5	Group 7 Upper Fraser
Quesnel River	83	11730	237.2	3.39	81-90	154.0	stream	9/25-10/2	5	Group 2 Middle Fraser
Raft River	84	764	15.2	7.67	80-89	NA	stream	9/9-9/16	5	Group 3 North Thompson
Robson River	85	NA	NA	NA	NA	NA	stream	9/2-9/9	5	Group 7 Upper Fraser
Salmon River (Prince George)	86	4437	24.3	7.24	81-90	NA	stream	8/23-8/30	5	Group 7 Upper Fraser
Salmon River (Salmon Arm)	87	1501	4.6	6.22	80-89	196.0	stream	9/11-9/18	5	Group 5 North-South Thompson
Scotch Creek	88	611	7.7	8.01	80-89	117.8	***stream***	10/2-10/9	***5***	Group 5 North-South Thompson
Seebach Creek	89	421	6.46	9.38	81-90	NA	stream	8/15-8/22	5	Group 7 Upper Fraser
Seton River	90	1920	28.5	5.26	81-90	193.5	stream	10/19-10/26	5	Group 2 Middle Fraser
Shuswap River (lower)	91	5415	101	4.16	80-89	196.4	ocean	10/6-10/13	4	Group 4 Lower-South Thompson
Shuswap River (middle)	92	NA	18.6	5.01	80-90	187.5	ocean	9/24-10/1	4	Group 5 North-South Thompson
Slim Creek	93	856	35.8	5.42	81-90	130.0	stream	8/26-9/2	5	Group 7 Upper Fraser
Sloquet Creek	94	206	24.3	7.67	81-90	NA	NA	late Aug/Sep	NA	Group 6 Lower-Middle Fraser
Small Creek	95	NA	NA	NA	NA	NA	stream	8/23-8/30	5	Group 7 Upper Fraser
Snowshoe Creek	96	100	4.18	5.43	81-90	NA	stream	8/14-8/21	5	Group 7 Upper Fraser
South Thompson River	97	17311	311	2.99	80-89	201.0	ocean	10/10-10/17	4	Group 4 Lower-South Thompson
Spius Creek	98	780	9.33	8.67	80-89	145.8	stream	8/27-9/3	4	Group 5 Lower Thompson

Stream Name	Number	Basin Area (km^2)	MAD (m^3/s)	Peak Flow Index	Record Period (years)	Mean G7 (days)	Juvenile Life History[1]	Peak Spawning (week)	Most Common Age at Return[1]	Biophysical Grouping
Stave River	100	1003	NA	NA	NA	NA	NA	NA	NA	Group 6 Lower-Middle Fraser
Stellako River	101	3600	15.75	3.03	81-90	160.9	***stream***	8/28-9/4	**5**	Group 2 Middle Fraser
Stuart River	102	NA	NA	NA	NA	NA	stream	9/10-9/17	5	Group 2 Middle Fraser
Swift Creek	103	135	3.19	8.12	81-90	NA	stream	8/16-8/23	5	Group 7 Upper Fraser
Tachie River	104	NA	NA	NA	NA	163.0	stream	NA	5	Group 6 Lower-Middle Fraser
Taseko River	105	2730	35.5	4.39	81-90	NA	stream	9/8-9/15	5	Group 2 Middle Fraser
Thompson River (lower)	106	55665	759	3.49	80-89	205.3	ocean	9/28-10/5	4	Group 4 Lower-South Thompson
Torpy River	107	1285	53.7	5.43	81-90	NA	stream	8/13-8/20	5	Group 7 Upper Fraser
Walker Creek	108	364	15.2	5.43	81-90	NA	stream	8/13-8/20	5	Group 7 Upper Fraser
Wansa Creek	109	293	4.49	9.40	81-91	NA	stream	8/24-8/31	5	Group 7 Upper Fraser
Wap Creek	110	354	14.9	6.91	80-89	NA	***stream***	9/14-9/21	**5**	Group 5 North-South Thompson
West Twin Creek	111	174	7.27	5.43	81-90	NA	***stream***	8/8-8/15	**5**	Group 7 Upper Fraser
Westroad River	112	12400	24.9	4.41	81-90	NA	stream	8/26-9/2	5	Group 6 Lower-Middle Fraser
Willow River	113	2875	36.5	7.04	81-90	NA	stream	8/24-8/31	5	Group 7 Upper Fraser
Yalakom River	114	676	4.11	5.52	81-90	NA	***stream***	8/24-8/31	***4***	Group 6 Lower-Middle Fraser

NA indicates systems with no data.

1. Bold and italics were used for systems with no scale samples, although juvenile life history and most common age at maturity were assumed to be similar to nearby spawning systems.

Appendix 2. Gradient, length, wetted width, spawner density and the maximum number of spawners estimated for survey strata.

River	Stratum	Gradient $G_{j,k}$	Length (m) $L_{j,k}$	Wetted Width (m) $\hat{W}_{j,k}$	Maximum Number of Spawners Max $\hat{N}_{i,j,k}$	Spawner Density ($\hat{D}_{j,k,l}$) Linear (spawners/km)	Area (spawners/m^2)
L. Shuswap	1	0.0004	1179	56.3	1630	1382.6	0.0246
L. Shuswap	2	0.0054	2344	59.0	75	32.0	0.0005
L. Shuswap	3	0.0021	2781	59.0	9299	3344.3	0.0567
L. Shuswap	4	0.0017	2719	59.0	9939	3654.9	0.0620
L. Shuswap	5	0.0024	5741	59.0	9907	1725.5	0.0293
L. Shuswap	6	-0.0002	2803	59.0	3774	1346.4	0.0228
L. Shuswap	7	0.0006	5858	59.0	565	96.4	0.0016
L. Shuswap	8	0.0004	4213	59.6	311	73.8	0.0012
L. Shuswap	9	-0.0004	2392	59.6	1562	652.9	0.0110
L. Shuswap	10	0.0000	4207	59.6	550	130.8	0.0022
L. Shuswap	11	0.0002	38316	59.6	0	0.0	0.0000
L. Shuswap	Sum of Strata	0.0006	72552	60.6	37611	518.4	0.0087
L. Shuswap	Maximum Escapement	0.0006	72552	60.6	37536	517.4	0.0087
Raft	1	0.0010	502	22.5	74	147.7	0.0066
Raft	2	0.0010	502	22.5	74	147.7	0.0066
Raft	3	0.0000	502	22.5	75	150.0	0.0067
Raft	4	-0.0010	502	22.5	112	222.6	0.0099
Raft	5	0.0070	502	22.5	181	361.1	0.0161
Raft	6	0.0030	502	22.5	834	1661.3	0.0738
Raft	7	0.0000	502	22.5	390	777.9	0.0346
Raft	8	0.0137	769	22.5	184	239.3	0.0106
Raft	Sum of Strata	0.0037	4282	22.5	1924	449.4	0.0200
Raft	Maximum Escapement	0.0037	4282	22.5	1371	320.2	0.0136
Clearwater	1	0.0028	42524	91.0	5663	133.2	0.0015
Clearwater	2	0.0038	7403	83.4	860	116.1	0.0014
Clearwater	3	0.0038	19523	70.8	5161	264.3	0.0037
Clearwater	Sum of Strata	0.0032	69450	91.0	11683	168.2	0.0020
Clearwater	Maximum Escapement	0.0032	69450	91.0	7830	112.7	0.0013
Mahood	Sum of Strata	0.0061	1545	34.1	415	268.6	0.0079
Mahood	Maximum Escapement	0.0061	1545	34.1	700	453.0	0.0133
Bowron	1	0.0009	33930	38.3	7016	206.8	0.0054
Bowron	2	0.0026	26690	44.2	1165	43.7	0.0010
Bowron	3	0.0019	46449	47.5	505	10.9	0.0002
Bowron	4	0.0030	44482	47.5	0	0.0	0.0000
Bowron	Sum of Reaches	0.0013	146852	47.5	8686	59.1	0.0013
Bowron	Maximum Escapement	0.0013	146852	47.5	10900	74.2	0.0016
Willow	1	0.0018	16035	35.6	16	1.0	0.0000
Willow	2	0.0026	15789	35.6	1396	88.4	0.0025
Willow	3	0.0023	7699	33.2	645	83.8	0.0025
Willow	4	0.0298	1461	33.2	0	0.0	0.0000
Willow	Sum of Strata	0.0032	40984	35.6	2057	50.2	0.0014
Elkin	1	0.0022	1352	8.0	88	65.1	0.0081
Elkin	2	0.0013	781	8.0	68	87.6	0.0110
Elkin	3	0.0002	2069	8.0	0	0.0	0.0000
Elkin	4	0.0030	4957	8.0	327	65.9	0.0083
Elkin	5	0.0017	1785	8.0	85	68.4	0.0086
Elkin	6	0.0189	4726	8.0	0	0.0	0.0000
Elkin	Sum of Strata	0.0044	15671	8.0	569	36.3	0.0036
Elkin	Maximum Escapement	0.0044	15671	8.0	1250	79.8	0.0078
Chilko	1	0.0000	342	54.1	10	29.2	0.0005
Chilko	2	0.0012	3340	54.1	1024	306.6	0.0057
Chilko	3	0.0043	3938	54.1	8859	2249.4	0.0415
Chilko	4	0.0064	4459	54.1	6053	1357.7	0.0251
Chilko	5	0.0099	11080	54.1	4252	383.7	0.0071
Chilko	6	0.0148	17637	54.1	1846	104.6	0.0019
Chilko	Sum of Strata	0.0104	40454	54.1	22043	544.9	0.0101

River	Stratum	Gradient $G_{j,k}$	Length (m) $L_{j,k}$	Wetted Width (m) $\hat{W}_{j,k}$	Maximum Number of Spawners $\text{Max}\,\hat{N}_{i,j,k}$	Spawner Density ($\hat{D}_{j,k,l}$) Linear (spawners/km)	Area (spawners/m^2)
Chilko	Maximum Escapement	0.0104	40454	54.1	17000	420.2	0.0078
Nicola	1	0.0012	28611	13.8	4522	158.0	0.0115
Nicola	2	0.0028	14150	21.0	7319	517.3	0.0246
Nicola	3	0.0036	8590	21.0	2992	348.3	0.0166
Nicola	4	0.0048	18958	27.7	1108	58.5	0.0021
Nicola	5	0.0051	8581	27.7	447	52.1	0.0019
Nicola	6	0.0069	23101	27.7	0	0.0	0.0000
Nicola	Sum of Strata	0.0039	101991	27.7	16388	160.7	0.0072
Coldwater	1	0.0050	27942	15.5	2203	78.8	0.0051
Spius	1	0.0093	6724	17.4	369	54.9	0.0032
Nechako	1	0.0020	2173	46.8	368	169.3	0.0036
Nechako	2	0.0013	3718	46.8	168	45.2	0.0010
Nechako	3	0.0001	3712	46.8	1302	350.8	0.0075
Nechako	4	0.0024	4764	46.8	862	180.9	0.0039
Nechako	5	0.0001	4963	46.8	559	112.6	0.0024
Nechako	6	-0.0005	3833	46.8	1005	262.2	0.0056
Nechako	7	0.0005	7113	46.8	841	118.2	0.0025
Nechako	8	0.0003	5795	46.8	243	42.0	0.0003
Nechako	9	0.0004	10670	46.8	191	17.9	0.0004
Nechako	10	0.0005	5616	46.8	214	38.0	0.0008
Nechako	11	0.0011	10172	46.8	440	43.2	0.0009
Nechako	12	0.0014	8092	46.8	668	82.5	0.0018
Nechako	13	-0.0002	5652	46.8	797	141.0	0.0030
Nechako	14	-0.0003	12240	46.8	283	23.1	0.0005
Nechako	15	0.0009	14692	54.9	555	37.8	0.0007
Nechako	16	0.0006	21056	54.9	439	20.9	0.0004
Nechako	17	0.0008	19922	54.9	653	32.8	0.0006
Nechako	18	0.0000	44535	54.9	0	0.0	0.0000
Nechako	Sum of Strata	0.0005	188717	54.9	9587	50.8	0.0010
Nechako	Maximum Escapement	0.0005	188717	54.9	9331	49.4	0.0010

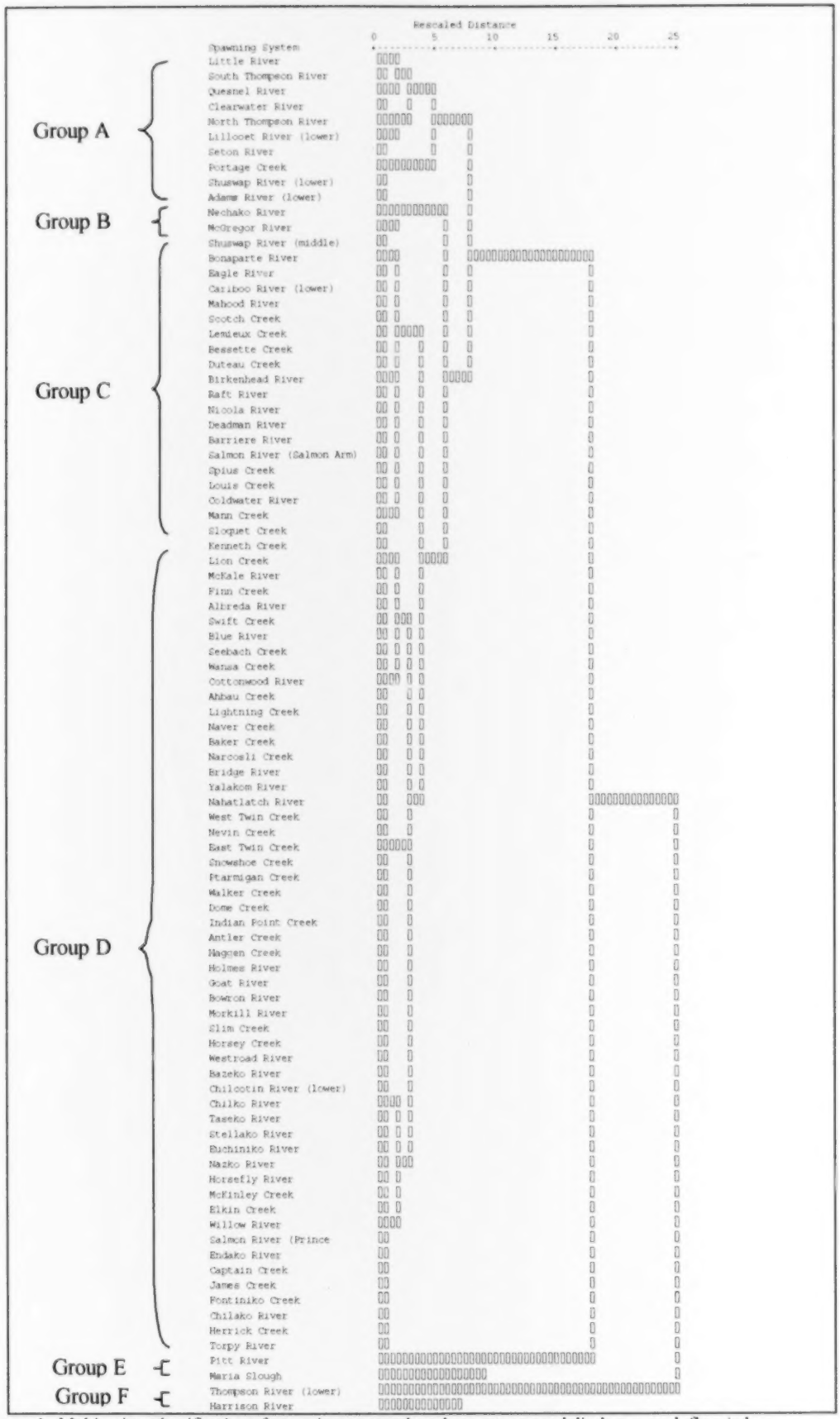
Appendix 3. Multivariate classification system.

A multivariate classification hierarchy was developed from environmental variables that may indicate where data pooling is reasonable. We conducted a cluster analysis using the average linkage between groups (UPGMA) method to clarify environmental relationships among spawning systems. To characterize spawning environments, we used the mean annual discharge, peak flow index, ecoprovince, and the week of the peak of spawning activity. Mean annual discharge indicates river size, and the nature of channel units (Hawkins et al. 1993) and thermal regime may depend upon river size. The peak flow index indicates the stability of the discharge regime and possibly the degree of bedload movement, erosion, or scour, which influence the spawning habitat quality and egg-to-fry survival. Ecoprovinces describe areas of broad physiographic and climatic uniformity of terrestrial variables (Meidinger and Pojar 1991), which can lead to insight into the broad habitat characteristics of water bodies (Meixler 1999). The timing of spawning activity indicates the incubation thermal regime since egg development is likely associated with degree-day accumulation and fry emergence in the spring (Burgner 1991). Several spawning systems were omitted because of sample size requirements.

There appear to be six main groups of spawning systems corresponding to general aquatic habitat characteristics (Appendix Figure 1). The first group (A) includes moderate-size rivers in warm environments with stable discharge regimes and peaks of spawning activity during September or October. Group B includes moderate-size rivers in cool environments with stable discharge regimes and peaks of spawning activity during September. Group C includes small rivers in warm environments with variable discharge regimes and peaks of spawning activity during September. Group D includes small to moderate-size rivers in cool environments with variable discharge regimes and peaks of spawning activity during August or September. Group E includes small rivers in warm environments with highly variable discharge regimes and peaks of spawning activity during September or October. The last group (F) includes large rivers in warm environments with very stable discharge regimes and peaks of spawning activity during October or November.

This classification scheme was based on a mixed data set of categorical (ecoprovinces) and continuous variables. This approach is generally not advised (McGarigal et al. 2000), but continuous variables for physiographic or climatic conditions were not available for all spawning systems. The classification structure may change with the inclusion of variables such as stream gradient, pool-riffle frequency, sinuosity, peak flood flow, a quantitative variable for lake moderating influence, or continuous variables for physiography or climate.

The multivariate classification developed fewer groups than the hierarchical stratification based on categorical biophysical characteristics (Figure 3). We were unable to assess which classification system was most appropriate because spawner capacity models were only available for the Nicola and Lower Shuswap rivers and gradient and length data were limited to the case study rivers. It may be beneficial to compare spawner capacity estimates developed from different classifications to assess the reliability of the approaches.



Appendix Figure 1. Multivariate classification of spawning systems based on mean annual discharge, peak flow index, ecoprovince, and the week of the peak of spawning activity.